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**Vegetation recovery following volcanic disturbance on
Mt. Tongariro, New Zealand**

A thesis
submitted in fulfilment
of the requirements for the degree
of
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at
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by
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Abstract

On August 6, 2012, a series of volcanic eruptions occurred on Mt. Tongariro in the central North Island of New Zealand. The eruptions included pyroclastic density currents (PDCs), a debris flow and volcanic projectiles, each of which significantly affected native vegetation. The present study investigated four aspects of vegetation dynamics in relation to the eruptions. First, the effect of PDCs on the subalpine conifer, *Phyllocladus alpinus*. Second, differential species sensitivity to the PDCs. Third, the species composition of the impact craters formed by volcanic projectiles, and the fourth aspect, colonisation of a newly formed debris flow.

Thirty *P. alpinus* individuals were sampled at twenty two plots throughout the area affected by the PDCs. The numbers of “Live” and “Dead” individuals within plots were significantly correlated with distance to the eruption, and tree height (a predictor of age). Smaller and younger *P. alpinus* were more likely to be “Live” while larger, older *P. alpinus* more likely to be “Dead”. This is most likely due to the exposure and temperatures associated with PDCs. The mean foliar cover for all “Damaged” individuals was 75.59% with these individuals significantly correlated to plot area and altitude. Increased light availability and the path of the PDCs may explain these findings.

Phyllocladus alpinus was the species most affected by the PDCs with only 57.73% foliar survival. Species sensitivity appears to be based on a combination of height and morphological features. Taller species are most affected by PDCs with small, coriaceous or glossy leaves; or narrow flexible leaves being advantageous. Stiff curved leaves, hairs, scales and a dense growth form appear detrimental to foliar survival.

Species richness and percent cover were measured, both inside and directly outside the impact craters in 2013, 2015 and 2017 respectively. Outside the craters there was an increase in species richness with each year of measurement, however, the percent cover decreased from 2013 to 2015 before increasing in 2017. This decrease is most likely attributed to a statistically significant decrease in the cover of *Dracophyllum recurvum*. Between 2013 and 2015 there was a decrease in both species richness and percent cover inside the craters. This trend reversed between

2015 and 2017 with a statistically significant increase in species richness, and an increase in percent cover. This suggests species survived the initial impact of the projectile but experienced subsequent dieback followed by regeneration.

Thirty 2 x 2 m sites were sampled on the debris flow, with nine sites containing vegetation. The overall colonisation rate was 0.14 species/quadrat per year, with *Poa* the most frequent and abundant genus. Topography, substrate particle size and proximity to seed sources appear to constrain seed dispersal and germination, resulting in varying and low rates of colonisation.

The present study highlights that species responses vary depending on the nature and magnitude of volcanic disturbance. Further research, including remeasurements, will continue to improve the understanding of mechanism/s that drive ecological succession after volcanic disturbance, and contribute to the development of future models of succession.

Keywords: *Phyllocladus alpinus*, succession, craters, pyroclastic density currents, projectiles, debris flow, eruptions, volcanic disturbance, Te Maari, Tongariro

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Chapter 1

Introduction

This thesis presents the results of my research investigating the impact of the 2012 eruptions near the pre existing Upper Te Maari crater, on the subalpine vegetation of Mt. Tongariro. Before presenting the results and analyses of the research, relevant background information on ecosystem responses, successional processes and the research area is provided. This chapter concludes by presenting the research objectives, questions, and outline of the thesis.

1.1 Ecosystem responses

Ecosystem responses to volcanic events vary with the type, scale, frequency and severity of the event/s. Understanding how these ecosystems on volcanic landscapes recover, informs us about fundamental ecological processes (del Moral & Grishin 1999), and contributes to the knowledge base required to form accurate models of succession.

Recovery on volcanic landscapes has a set of common parameters; “Plant responses to a given impact depend on their size and growth form. At a sufficient distance from the cone, directed blasts and pyroclastic events will most severely impact taller vegetation. Ground layer and juveniles may be protected by topography, while buried structures are protected by soil. Dormant plants will be more likely to survive, and a snow pack will enhance survival. Species with seed banks are more likely to dominate recovering vegetation” (del Moral & Grishin 1999). These parameters however have not led to a common model of plant succession.

1.2 Successional processes

Ecological succession, including plant succession, is the process by which the structure of a biological community evolves over time (Thompson 2016). There are two types of plant succession, primary and secondary successions.

Primary succession is succession beginning on newly produced bare areas (Allaby

2012) where existing plant material and propagules have been removed or buried leaving “little or no biological legacy” (Walker & del Moral 2011). The successional mechanisms that can produce habitats suitable for primary succession included lava flows, debris flows and the intra-crater space of an impact crater formed by ballistic projectiles.

Secondary succession is succession in which the primary succession or late successional vegetation has been disrupted or disturbed (Allaby 2012). Biological legacy in the form of surviving plants or propagules set secondary succession apart from primary succession. Events associated with volcanic eruptions such as ash fall, PDCs and displaced substrate from ballistic projectiles (for example the debris aprons associated with the outside of impact craters) can all be mechanisms for secondary succession.

Successional mechanisms and pathways associated with volcanic disturbances can vary with both primary and secondary succession (del Moral & Grishin 1999) and as such, “Plant successions on volcanic substrates are extremely variable both in terms of rates and the sequence of species establishing” (Clarkson 1990). This variability has led to a difficulty in establishing a common model of succession for volcanic ecosystems. Secondary successions with partial volcanic disturbance are extremely difficult to fit into successional models (Clarkson 1990) as the majority of successional models begin with primary succession, referring to secondary succession as a change in these models.

1.2.1 Historical overview of Successional Models

Successional models began with Clements (1916), who suggested succession was a directional process resulting in a stable climax community. This theory included the following processes:

- 1: Nudation – a disturbance which removed all vegetation, creating bare ground
- 2: Migration – the arrival of propagules to the site
- 3: Ecesis – the establishment and initial growth of vegetation
- 4: Competition – interspecific competition between plants for resources
- 5: Reaction – the change in environment as a result of plant growth and death
- 6: Stabilization – the community reaches an equilibrium, resulting in a climax community.

The driving mechanisms were thought to be autogenic processes, with species altering site conditions making it more suitable for other species to colonise (Walker & Del Moral 2003). This traditional view dominated successional theory for 50 years (Glenn-Lewin & van der Maarel 1992) before being rejected as “not wholly applicable to observed vegetation change” (Clarkson 1990).

Connell and Slatyer (1977) stated there was evidence for 3 models of succession:

- 1: Facilitation (also known as relay floristics) – suggests colonists prepare the habitat for late succession species
- 2: Tolerance – species sequence is solely a function of life history
- 3: Inhibition – once colonists establish, they inhibit invasions by other species.

These models were also reviewed and described as not being wholly representative of succession (McIntosh 1981; Finegan 1984; Pickett et al. 1987).

Tilman (1985) presented “an alternative, simple theory of succession, the resource-ratio hypothesis”, in which interspecific competition for resources is considered the driving mechanism. This hypothesis “assumes that competition is the principal selection pressure at all times during primary succession, and that resource acquisition is a continuous process” (Caccianiga et al. 2006). Contrary to this view Caccianiga et al. (2006) found that for alpine plants, resource acquisition and growth were not continuous. They speculated that abiotic factors overrule biotic interactions as a driving mechanism when plants are seasonally covered by snow or experience frozen soil.

Finegan (1984) suggested that successional processes and therefore models may not be mutually exclusive, with multiple models applicable in a single system. This concept was supported by Clarkson (1990) who found that “some primary successions, for example on the dome tops of Tarawera have elements for facilitation, autogenic change and relay floristics”. Walker et al. (2003) also supported this concept when examining whether nitrogen-fixing plants facilitate or inhibit species change in primary succession: “Sequential facilitative events determine the order of species replacements in this study but inhibition, linked to the developmental stages of *Coriaria*, may determine the rate of species change”.

Present day theories and models to describe primary succession are still developing as more studies into primary succession are conducted and reviewed. These studies are important for our understanding of fundamental ecological processes and specifically, the dynamics of active volcanic landscapes (del Moral & Grishin 1999).

1.3 Research Area

The Tongariro National Park (TNP) is located in the Central North Island of New Zealand (Figure 1.1).

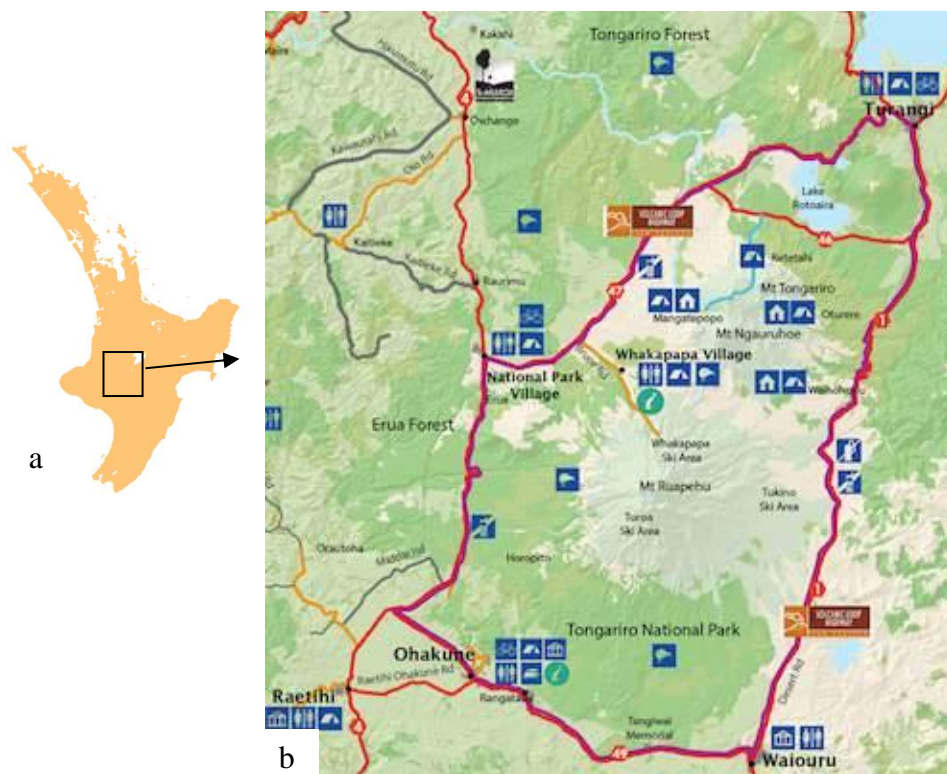


Figure 1.1 Map of the Tongariro National Park, North Island, New Zealand. Image (a) sourced from <https://en.wikipedia.org/wiki/Pihanga>. Image (b) sourced from <http://riverstonebackpackers.com/wp-content/uploads/2015/03/tongariro-national-park.jpg>

The TNP is New Zealand's oldest National Park (Department of Conservation 2017b) and a U.N.E.S.C.O. World Heritage Area (Jolly et al. 2014). It is classified as a “dual world heritage site” being recognised for both its cultural and natural significance (Williams 2013), including its geological and ecological values (U.N.E.S.C.O. 2017). Approximately one million people visit the TNP every year, (Department of Conservation 2017a), mainly visiting during the summer, and many of whom walk the popular Tongariro Alpine Crossing track over Mt. Tongariro. Mt. Tongariro is an active compound volcano reaching 1967 m a.s.l (above sea

level) (Department of Conservation 2017a). The prevailing winds are westerlies and north westerlies, with rain fall approximately 2000 mm a year. Daily temperatures can vary significantly with the extremes of 25°C in the summer and -10°C in the winter. Snow can fall any time of the year but the majority falls in winter, to an average of 1500 m a.s.l. (Department of Conservation 2017c).

A comprehensive botanical survey of the TNP was conducted between 1960 and 1966 (Atkinson 1981). The survey showed the vegetation adjacent to State Highway 46, between 600 and 1000 m a.s.l., is scrub, dominated by *Leptospermum scoparium* (mānuka) and *Kunzea ericoides* (kānuka). Heading towards the summit, between 700 and 1100 m a.s.l., the vegetation changes to native forest that is predominately *Podocarpus hallii* (Hall's tōtara). There are also pockets dominated by *Dacrydium cupressium* (rimu) and *Weinmannia racemosa* (kāmahī) between 600 and 950 m a.s.l. that contain individuals over 500 years old. The vegetation returns to scrub between 800 and 1250 m a.s.l., this time containing predominately *Phyllocladus alpinus* (mountain toatoa) and *L.scoparium*. Tussock-shrublands are then found between 1050 and 1600 m a.s.l., with *Dracophyllum longifolium* (inaka) and *Chionochloa rubra* (red tussock) dominating the landscape. Areas near, and including the summit, are relatively devoid of vegetation, with *Rhacomitrium* as the common genus.

This internationally recognised landscape was changed on the 6th of August 2012, through a series of three volcanic eruptions within 20 seconds . These eruptions were located near the pre existing Upper Te Maari crater, on Mt. Tongariro (Jolly et al. 2014) (Figure 1.2). The eruptions produced:

- A debris flow stretching 2.04 km that covered an area of 151 000 m² (Procter et al. 2014) and blocked three tributaries, one of which led to a significant impoundment of water that broke out on 13 October, 2016 and caused a major secondary lahar that smothered vegetation (Jolly et al. 2014).
- Approximately 13,200 ballistic projectiles (Fitzgerald et al. 2014) resulting in >2200 impact craters with diameters >2.5 m (Breard et al. 2014).
- Pyroclastic density currents (PDCs) or pyroclastic surges with initial estimated velocities of 55 - 115 m/s in various directions (Lube et al. 2014) over a timespan of approximately 60 seconds, with estimated temperatures near the vent >64 °C and estimated distal temperatures >51 °C (Efford et al.

2014).

- The excavation of new fissure-like craters (Procter et al. 2014).
- The ejection of ash at least 7.8km above the vent which travelled up to 200 km eastwards. The ash travelled at approximately 80 km/h over as much as 6000 km² (Pardo et al. 2014), with a minimum volume of 231,000 – 280,400 m³ (Procter et al. 2014).

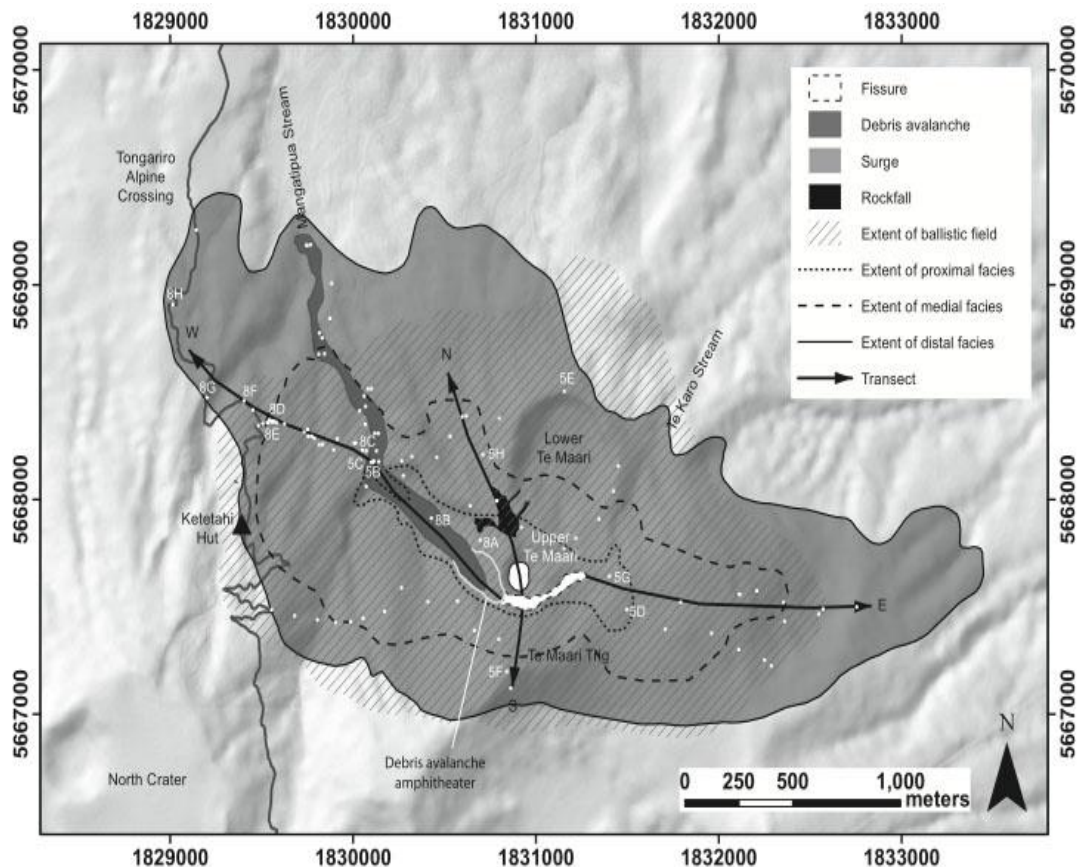


Figure 1.2 Details of areas effected during the August 2012 Te Maari eruption. Image sourced from Lube et al. (2014)

An eruption followed on the 21st of November 2012, however this was less intense and only released a small amount of ash (Scott & Potter 2014), towards the southwest (Pardo et al. 2014).

Examination of the vegetation by Efford et al. (2014) in the months following the August eruptions, showed multiple vegetation zones had been affected, including forest, scrub, tussock-shrublands and tussocklands. The tussock-shrublands to the northwest of the vent were one of the most severely affected areas, displaying widespread dieback (characterised by dead brown foliage), over a large area. The

extent of the damage appeared to vary with distance to the eruption crater and the species involved. There were “obvious differences in species susceptibility to the PDCs. For example, at the distal ends of the PDCs it was possible to find a completely browned apparently dead *Phyllocladus alpinus* tree alongside green and apparently unaffected *Podocarpus nivalis* sub-shrubs, while in the mid portions of the PDC, both of these species exhibited complete foliar browning” (Efford et al. 2014). Although this suggests *P. alpinus* was one of the species most affected by the PDCs, these observations were not quantified and therefore became a focus of investigation for future research. Documenting which species were the most affected, and monitoring these species over time will help provide an understanding of how volcanic disturbance affects secondary succession in a tussock-shrubland community.

Phyllocladus alpinus is an important native species and is located on most mountain ranges in the North Island. It can thrive in a range of ecosystems, from open vegetation to forests, and bare rock to wet ground. In primary succession habitats, *P. alpinus* often appears as an early successional species, which then persists through to the climax. In the TNP there is a long history of eruptions and fires that have created ecotones between tussock-grassland or scrub, and dense Podocarp forest. *Phyllocladus alpinus* is often abundant in these ecotones and can act as a nurse plant for podocarp seedlings (Wardle 1969). Due to its significance in the landscape and as a successional species, *P. alpinus* was selected as the focus species for the present study.

Efford et al. (2014) noted that within three months of the August eruptions, vegetation recovery within the affected area (hereby known as eruption zone) had already begun. Some individuals that were entirely browned after the eruption were resprouting new foliage from the thicker, central stems (rather than the branch extremities). The identification of which species were exhibiting this resprout was not stated, nor was the location of these individuals (i.e. in relation to the distance from the eruption). An investigation into the survival and level of resprout for each species would be a large task. Examining the survival and foliar damage of a known affected species such as *P. alpinus*, was a viable research opportunity. This would also provide valuable information regarding how vegetation recovers after a volcanic disturbance.

The ballistic projectiles that were ejected during the August eruptions, created impact craters within the tussockland west of Te Maari. During this process many species were effected, either by the direct impact or through the displacement of the substrate. This resulted in the intra-crater space becoming a possible habitat for primary succession, while the area directly outside the craters a habitat for secondary succession. Staff and students associated with the University of Waikato recognised this unique opportunity and recorded the species richness and percent cover, inside and directly outside, 15 of these craters. These measurements were recorded in 2013 and 2015. A repetition of measurements, particularly at equal time intervals, would provide invaluable quantitative data towards understanding how successional pathways vary, for primary and secondary successions within the same vegetation type, after volcanic disturbance.

The debris flow that occurred during the August eruptions also significantly damaged the surrounding vegetation. The section of the debris flow closest to the vent received the largest volume of deposit, with the newly formed surface being a habitat for primary succession. The opportunity to research on such surfaces are rare, and would again provide invaluable quantitative data for discussions around the type and rate of species involved with primary succession after volcanic disturbance.

1.4 Research Aim, Objectives and Questions

The aim of the present research is to enhance the understanding of how volcanic disturbance affects ecological successions, as well provide the kaitiaki of Mt. Tongariro with quantitative data for management decisions.

There are two main research objectives in this thesis. The first objective is to determine how *P. alpinus* and the surrounding species have responded to the PDCs. The second research objective is to investigate the colonisation and species composition of the impact craters and newly formed debris flow. These objectives are addressed by considering the following research questions:

Chapter Two:

1. Does the survival of *P. alpinus* vary within the eruption zone, and which variables are correlated with this survival?
2. Does the age of *P. alpinus* influence the survival state, and if so which variables are correlated with this survival?
3. What is the rate of resprout for “Damaged” *P. alpinus*, and does the age of *P. alpinus* effect this rate?

Chapter Three:

4. Was *P. alpinus* the species most affected by the volcanic disturbance?

Chapter Four:

5. How has the species composition associated with the impact craters changed over time?

Chapter Five:

6. Which plant species have colonised the surface of the debris flow?
7. What is the extent of colonisation?

1.5 Outline of Thesis

Chapter One: Introduction.

This chapter provides the relevant background information on the research area and the ecological concepts that underpin the context for this thesis. The research objectives, aims and outline are also provided in this chapter.

Chapter Two: Response of *Phyllocladus alpinus* to the 2012 Te Maari eruptions

In this chapter, the response of *P. alpinus* as the focus species is discussed. This includes the survival of *P. alpinus*, the influence of age, and the rate of resprouting. Analysis is primarily based on the life state of *P. alpinus* (“Live”, “Dead” or “Damaged”) within population structures, and direct measures.

Chapter Three: Species sensitivity to the 2012 Te Maari eruptions

The proportion of alive and dead material for each species is presented to determine which species were most affected, and therefore the most sensitive, to the volcanic disturbance. Factors explaining the different susceptibility of species are discussed.

Chapter Four: Vegetation development of impact craters formed by the 2012 Te Maari eruptions

This chapter presents the summary of findings, over a four year period, of the species richness and percent cover both inside and directly outside impact craters formed by ballistic projectiles. Results are compared both nationally and internationally.

Chapter Five: Vegetation development on a debris flow formed by the 2012 Te Maari eruptions

In this chapter, the species composition of the newly formed debris flow is presented. This includes which species have colonised, the level of colonisation and the distribution of those species. Dispersal characteristics of each of the species, and the germination on specific substrates, are considered to explain the current pattern.

Chapter 6: Synthesis

This chapter is a summary of the main findings from the present research. It provides discussions and recommendations for future research, for each chapter presented in this thesis.

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Chapter 2

Response of *Phyllocladus alpinus* to the 2012 Te Maari eruptions

2.1 Introduction

This chapter presents my research investigating the response of *Phyllocladus alpinus* to the volcanic disturbance of the 2012 eruptions on Mt Tongariro. Before presenting the research, relevant background information on *Phyllocladus alpinus* and pyroclastic density currents are provided.

2.1.1 Overview of *Phyllocladus alpinus*

Phyllocladus alpinus is more commonly known as mountain celery pine or mountain toatoa (Figure 2.1).



Figure 2.1 *Phyllocladus alpinus*. Photograph (a) “about 8 m tall and 15 cm dbh with several trunks, growing low on west side of Mt. Ruapehu [C.J. Earle, 2003.03.09]” sourced from http://www.conifers.org/po/Phyllocladus_alpinus.php. Photograph (b) Male strobili and phylloclades, photographed by Phil Bendle sourced from <http://www.terrain.net.nz/friends-of-te-henui-group/trees-native-botanical-names-m-to-q/mountain-toatoa-phyllcladus-aspleniifolius-var-alpinus.html>. Photograph (c) above 1000 m on Mt Tongariro.

A conifer in the Podocarpaceae family, *P. alpinus* is one of three named *Phyllocladus* species native to New Zealand (New Zealand Plant Conservation Network 2017). It is a dioecious shrub or small tree growing up to 9 m in height, with a short trunk, up to 40 cm in diameter (Wardle 1969). The wood has elastic properties which minimizes damage from wind (Allan 1961, Salmon 1996, as cited in Earle 2017). Stems in contact with the ground freely produce adventitious roots, with layering prevalent (Wardle 1969). True leaves are only present in seedlings and occasionally in young plants. They are up to 1.5 cm long, narrow-linear, acute and deciduous (Earle 2017). Juvenile to mature individuals possess phylloclades (specialised flattened stems) which appear as, and perform, the same function as leaves (Metcalf 2002). These are alternate to sub opposite with a short rachis (Allan 1982). Phylloclades vary in size and shape but are generally coriaceous (leathery) (Metcalf 2002). In juveniles, phylloclades are up to 2 cm long, thin, deeply divided, with narrow-linear segments and glaucous underside (Allan 1982). Adults possess phylloclades which are usually 1 - 2.5 cm long and 2 cm wide, but can grow up to 6 cm long. They are thick and coriaceous (Allan 1982). Shape variations include “narrow-rhomboid or spatulate, sparingly or much lobed, often elliptic to obovate, cuneate at base, apex subacute to broad-obtuse, margins crenate, leaf-denticles small” (Wardle 1969; Earle 2017). Female flowers arise along the margins of the phylloclades while male strobili (cones) are produced in clusters of 2 - 5 on the tips of branchlets (Metcalf 2002). The maximum life span of *P. alpinus* recorded to date is 260 years (Dunwiddie 1979, as cited in Wardle 1991).

P. alpinus is located in both the North and South Islands of New Zealand, from latitude 36° 50' southward; primarily between 900 and 1600 m a.s.l, but occur down to sea level in South Westland and Southland (Allan 1961, Salmon 1996, as cited in Earle 2017). *P. alpinus* prefers a mean annual temperature of 8.7 °C (Biffin et al. 2011, as cited in Earle 2017), with the freezing resistance ranging from -10 °C to -23 °C at 30 m and 1200 m a.s.l. respectively (Sakai et al. 1981). The mean annual precipitation preference of *P. alpinus* is 2705 mm (Biffin et al. 2011, as cited in Earle 2017).

Most *P. alpinus* in the Tongariro National Park (TNP) have phylloclades 6 - 28 mm long which are often conspicuously waxy (Wardle 1969). The species is common in the alpine and subalpine shrublands of the TNP. Walking up to the Ketetahi hut,

from State Highway 46, *P. alpinus* can be observed in the forest growing up to 9 m, then diminishing in stature (Earle 2017) as the altitude increases.

2.1.2 Pyroclastic Density Currents (PDCs)

Pyroclastic density currents (PDCs) or pyroclastic surges or flows are a “highly dangerous phenomena of explosive volcanic eruptions” (Lube et al. 2014). They are hot, fast moving currents (Brown 2017) consisting of a mixture of gas and solid (pyroclastic) particles ejected during an eruption (Sulpizio et al. 2014). Temperatures are often over 700°C (Dale et al. 2005), while speeds can reach up to 300 m/s (Valentine 1998), similar to hurricane velocities (Brown 2017). They move due to density contrasts between the atmosphere and the current (Andrews & Manga 2011). As they are under the effect of gravity, they move across the ground (Sulpizio et al. 2014; Brown 2017), although they can have enough force to “jump” over ridges (Dale et al. 2005). They can travel for a up to 100 km (Brown 2017), with their run out distances based on their mass, energy produced from the eruption, the energy loss to frictional processes (Sulpizio et al. 2014) and energy loss traversing ridges (Andrews & Manga 2011).

These PDCS can cause damage similar to a nuclear weapon (Valentine 1998). For humans, most deaths from volcanic eruptions (excluding famine and tsunamis) have been from PDCs (Baxter 1990). The high temperatures and associated particles can cause death by thermal injury and asphyxia, as they can readily burn and cause abrasions to skin and airways (Baxter 1990). For plants, PDCs have completely removed trees and other vegetation. The speed of particles suspended in the currents have “sand blasted” sections of wood from the side of trees while the high temperatures can kill trees by disturbing the hydrated tissues. Charred and singed vegetation are a common feature after PDCs (Blong 2013).

Two PDCs were produced on the 6th of August 2012, which contained over 330,00 m³ of eruption products (Lube et al. 2014). One PDC was directed east and the other west (Lube et al. 2014, as cited in Breard et al. 2014). The westward PDC was approximately 60 seconds in duration, with estimated temperatures near the vent >64 °C and >51 °C at the distal end (Efford et al. 2014). The PDC was estimated to have initially travelled between 55 - 115 m/s (Lube et al. 2014).

2.1.3 Effect of PDCs on *Phyllocladus alpinus*.

Heat from the westward PDC was considered to cause the wide spread die-back (characterised by foliage browning, Figure 2.2) of many species within the tussock-shrublands to the northwest of Te Maari, including *Phyllocladus alpinus* (Efford et al. 2014).



Figure 2.2 Foliage browning of vegetation, particularly *Phyllocladus alpinus* near the Tongariro Alpine Crossing track after the 2012 eruption on Mt. Tongariro. Photographs by Jackson Efford.

In the present day, widespread death (characterised by no foliage, Figure 2.3) is a common site in these tussock-shrublands, with brown phylloclades visible below many individuals, indicating the phylloclades browned by the PDC abscised.

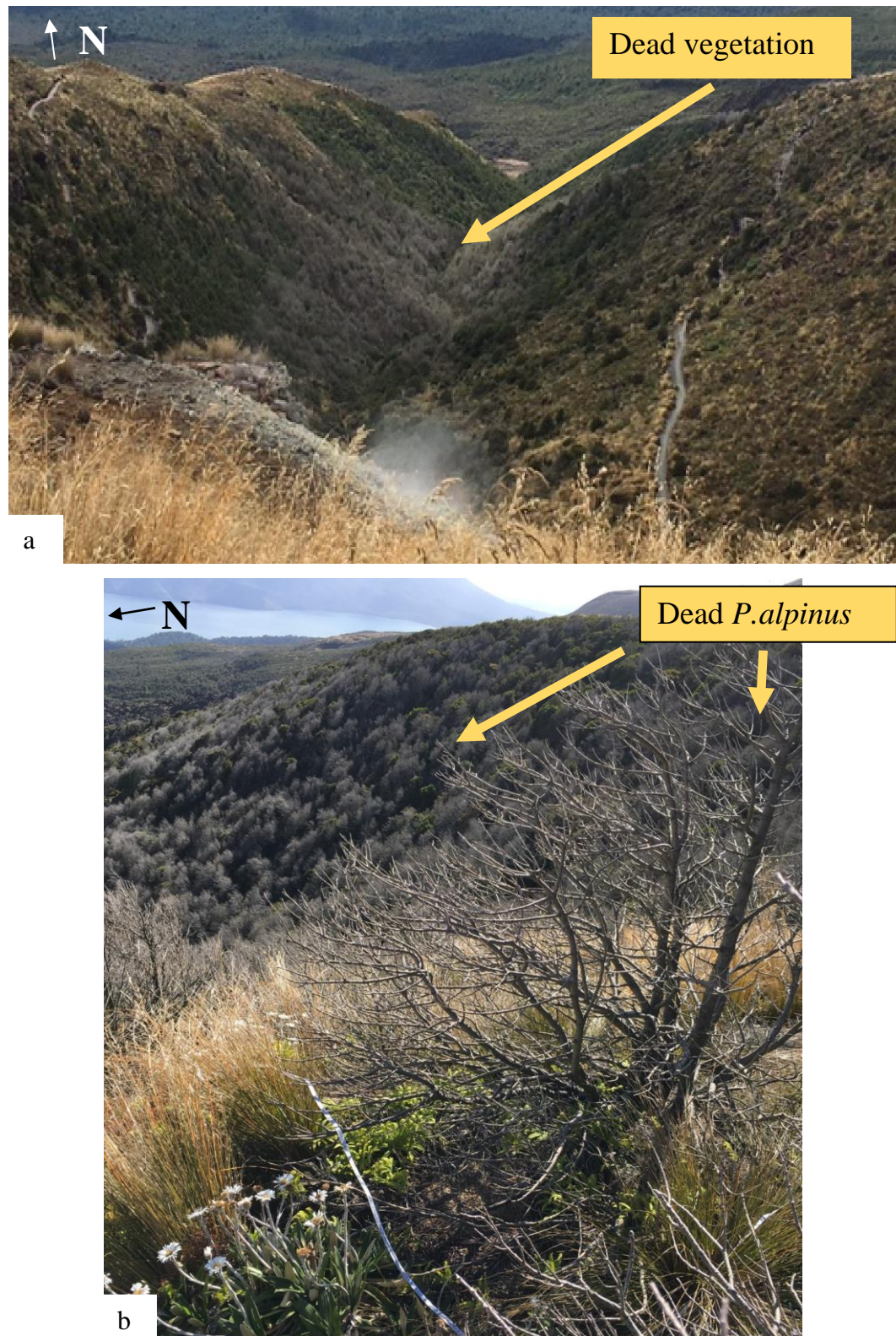


Figure 2.3 Photographs showing areas of dead vegetation (including *P.alpinus*) in the present day.

Phyllocladus alpinus appears to be the species most affected by the eruptions, with areas of dead vegetation containing a high proportion of this species. Currently some *P. alpinus* show signs of recovery (characterised by resprouting), and others appear unaffected (characterised by the presence of green foliage to the end of all branches, Figure 2.4). Survival appears to be correlated with the distance to the eruption (Upper Te Maari), with a higher proportion of dead individuals closer to Te Maari.

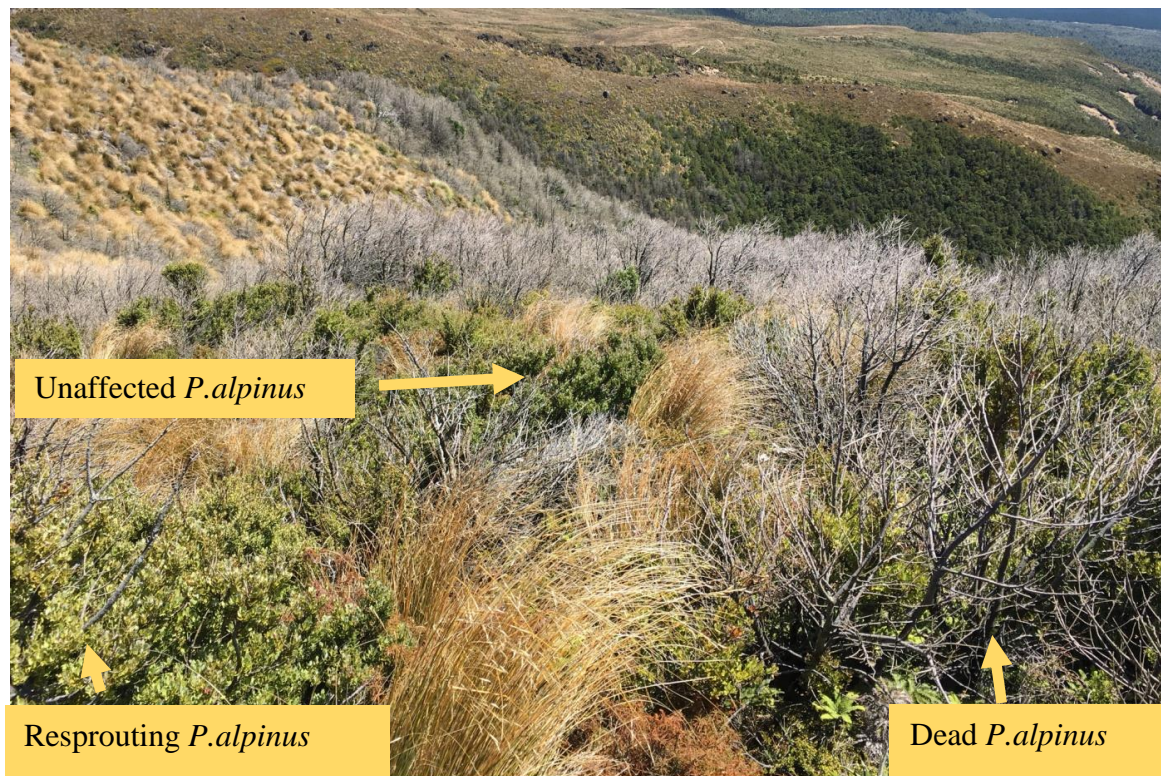


Figure 2.4 Photograph illustrating the different life states of *P. alpinus* in the present day.

The objective of this study was to provide quantitative evidence on how *P. alpinus* has responded to volcanic disturbance by considering the following research questions:

1. Does the survival of *P. alpinus* vary within the eruption zone, and which variables are correlated with this survival?
2. Does the age of *P. alpinus* influence the survival state, and if so which variables are correlated with this survival?
3. What is the rate of foliar recovery for damaged *P. alpinus*, and does the age of *P. alpinus* effect this rate?

2.2 Method

The research area is located below the Ketetahi Hut, near the Tongariro Alpine Crossing track, indicated by the red box in Figure 2.5 (for overview of the entire study area see Figure 1.2, Chapter 1). The area was selected for two reasons. Firstly, it contains the largest volume of *P. alpinus*, and secondly it spans the area affected by the eruptions and therefore includes *P. alpinus* close to Te Maari and at the distal end of the affected area (hereby called eruption zone).

The plots sampled spanned approximately 1000 - 1300 m a.s.l. Plot locations were selected using an online random number generator (<http://numbergenerator.org>). Two, three digit numbers were generated per plot using this online tool. The first number generated was between 048 and 997. This number was added to the prefix 1829 to create a New Zealand Transverse Mercator easting GPS co-ordinate. For example if the number 566 was selected the easting co-ordinate would be 1829566 (1829 were the constant first four digits for all easting co-ordinates throughout the research area). The second randomly generated number was between 200 and 768. This number was added to the prefix 5668 to create a New Zealand Transverse Mercator northing GPS co-ordinate (first four digits for any northing co-ordinate throughout the research area were 5668). Combining these easting and northing co-ordinates allowed for precise and randomly selected plot locations within the boundaries of the research area. A Garmin Oregon 750t Handheld GPS was used to locate plot co-ordinates. To ensure safety on the mountain and minimise the influence of human activity, the following criteria were set:

- 1: Thirty *P. alpinus* had to be measured within a 15 m radius.
- 2: No part of a plot was to be with 5 m of the Tongariro Alpine Crossing track.
- 3: Plots must not overlap in range.
- 4: Plots had to be safe to sample (i.e. not close to a cliff or too steep to safely traverse).

Plots which did not meet these criteria were eliminated and new plots selected.

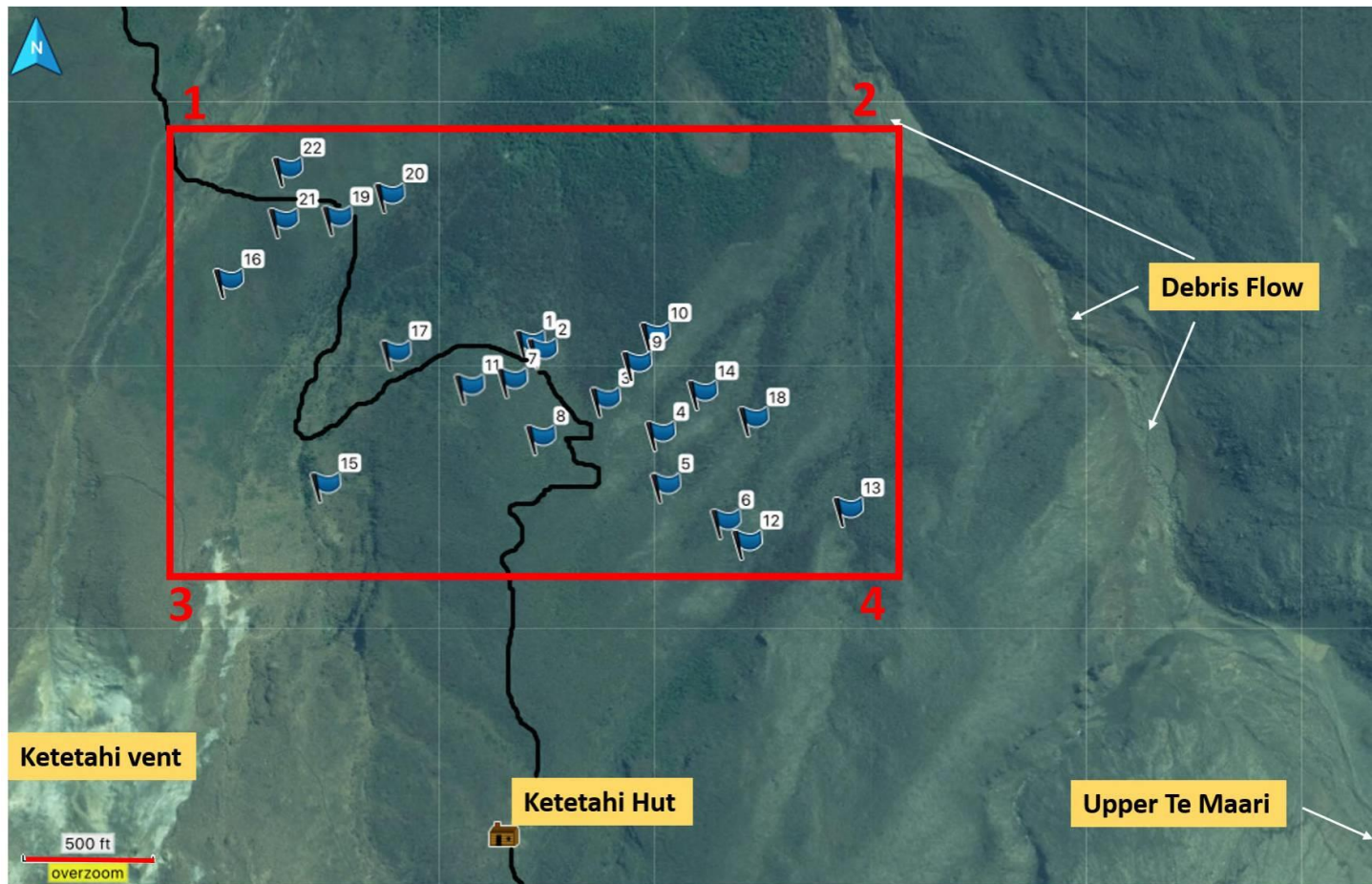


Figure 2.5 Location of plots on Mt. Tongariro. Red box indicates the limits of the research area. The New Zealand Transverse Mercator GPS co-ordinates of the corners of these outer limits are: 1) 1829048 5668768, 2) 1829837 5668699, 3) 1828997 566822 and 4) 1829864 5668200.

This process was repeated until 22 suitable sites were identified (the maximum number of sites possible within the time and weather constraints on this research). Once a plot was considered suitable, a centre stake was placed into the ground. If an object, such as a boulder, was present at the precise GPS location, the stake was placed into the ground at the closest northern point to the object. Four, 30 m Fuller brand measuring tapes were then connected to the central stake and placed over top of the vegetation, in the directions of north, south, east and west (Figure 2.6).



Figure 2.6 Central stake and placement of measuring tapes over the vegetation at Plot 1.

The closest *P. alpinus* to the centre stake was then selected, and using the closest measuring tape, the distance from the centre stake to the *P. alpinus* was recorded. The direction of the individual from the central stake was then recorded using a Silva Expedition S Compass. The following additional measurements were also collected for each *P. alpinus*:

1. **Height of individual:** Measured from the ground to the individual's highest point, using a Fullers (brand) 5 m retractable measuring tape (Figure 2.7).

2. **Height of foliage:** Measured from the ground to the highest point in which live foliage was located on the individual (Figure 2.7). This measurement was collected using a Fullers (brand) 5 m retractable measuring tape.
3. **Crown width:** Measured using two perpendicular measurements from the widest points on each side of the individual (Figure 2.8), using a Fullers (brand) 5 m retractable measuring tape. Broken branches were excluded.
4. **Percent cover of foliage:** Visual estimation, from a bird's eye view, of the percentage of crown area covered in foliage. The primary researcher conducted all measurements to minimise bias. Broken branches were excluded.
5. **Basal diameter:** The basal diameter of each stem was recorded approximately 2 cm above the surface of the substrate, using a fibreglass diameter tape (brand unknown). If stems were too close to place the tape between, the tape was placed around the collection of stems as a "best measure" approach. As *P. alpinus* often layers, each stem needed to be established as either a new individual (stem direction was straight down), or a branch from another individual (curving back to another stem/trunk). This required using a finger to dig just below the soils surface (maximum 5 cm) and check the direction of the stem. To ensure the root systems of layered individuals were not disturbed, only the topside of stems were examined to establish the direction of growth (Figure 2.9).
6. **Direction of resprout:** The direction of resprout growth was recorded to the closest 1/8 direction e.g. N, NE, E, SE, S etc.
7. **Maximum basal sprout length:** The length of the longest sprout from the central trunk was recorded using a Fullers 5 m retractable measuring tape.
8. **Topography:** A description of the topography where the individual was located (i.e. flat, slope, bottom of a bank etc).



Figure 2.7 Annotated photograph illustrating the height of individual and height of foliage measurements.

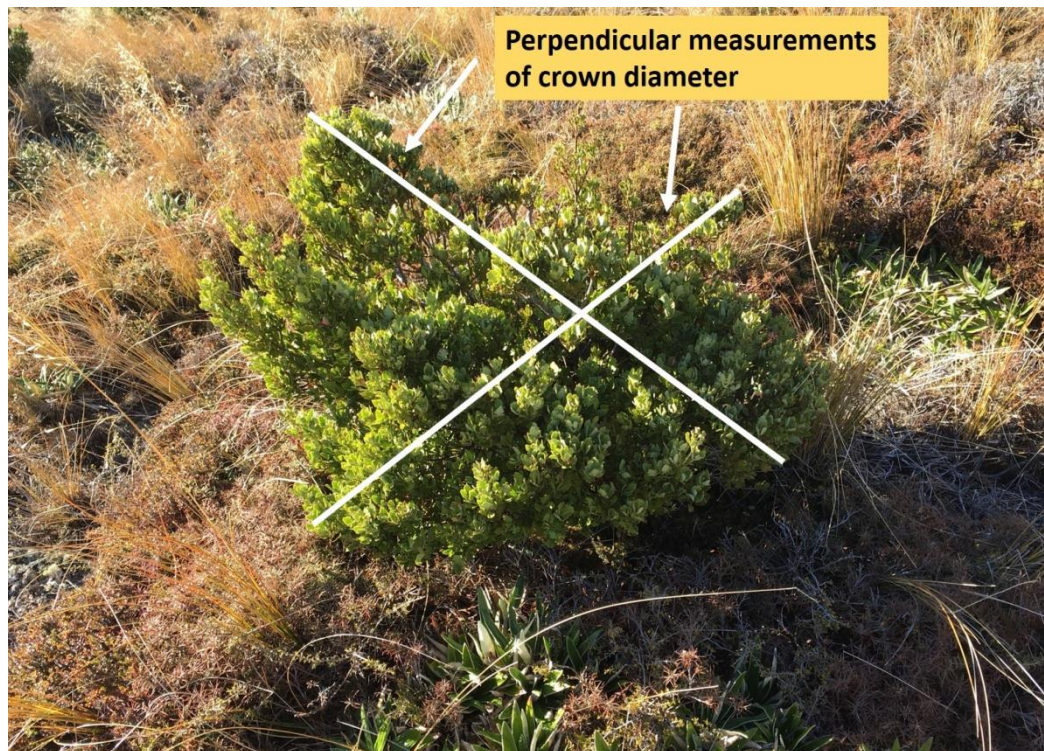


Figure 2.8 Annotated photograph illustrating the crown diameter measurements.

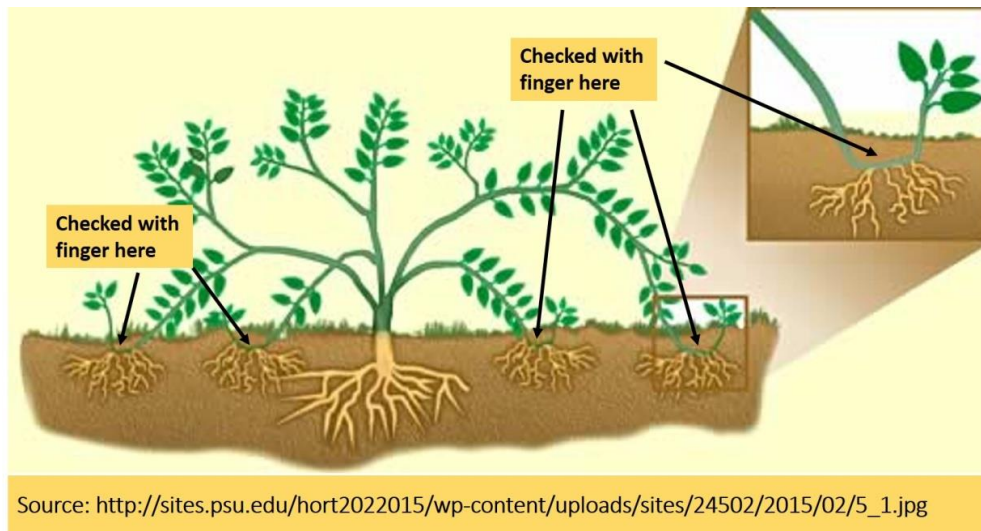


Figure 2.9 Visual illustration of where stems were checked to establish if they were a new individual or a branch from another individual.

A removable identification tag was then placed on the *P. alpinus* to ensure measurements for that individual were recorded once only. The processes outlined were repeated until the closest 30 individuals to the central stake had been identified and measurements recorded. This constant count method of thirty individuals was based on Jane (1982) and exceeds the 15 - 20 individuals required for the count size to be robust. Once all measurements for the 30 *P. alpinus* were recorded, the identification tags were removed and the maximum slope for the plot was recorded. This required two personnel standing on opposite sides of the plots perimeter (distance from centre for each person was the longest distance recorded for a *P. alpinus* to the central stake). The primary researcher then used the clinometer on the Silva Expedition S Compass to record the slope. This was recorded from the eye level of the primary researcher (1.65 m) to the same height on the other person (e.g. to top of the second persons head or to their eye level). This resulted in a parallel slope with the ground. The aspect and altitude of each plot was also recorded, aspect was determined visually, altitude was measured using a Garmin Oregon 750t Handheld GPS used unit.

Upon the completion of field measurements, the plot area was calculated for all plots using the formula $\pi=r^2$. In addition, a “survival percentage” was calculated for each *P. alpinus* based on their total foliage cover, using the following formula:

$$\frac{(\text{Height of foliage/height of the individual} \times 100)}{\text{percent foliage cover}}$$

2

This “survival percentage” was used for the classification of *P. alpinus* into one of three life states. A survival of 0% classified *P. alpinus* as “Dead”, a survival of 1-99% classified *P. alpinus* as “Damaged”, and a survival of 100% classified *P. alpinus* as “Live”. As these classifications are based on an individual’s total foliage cover, “Dead” individuals were characterised as possessing no green foliage, “Damaged” individuals displayed some green foliage (either existing and/or resprouted) and “Live” were completely covered in green foliage (assumed to be existing foliage).

Individuals were then placed into one of nine height categories (1-50 cm, 51-100 cm, 101-150 cm, 151-200 cm, 201-250 cm, 251-300 cm, 301-350 cm, 351-400 cm and 400+ cm) to determine a population structure by life state. Although conifer age is correlated to both height and diameter (Schuster & Oberhuber 2013), height was used as a predictor of age in this study, as accurate basal diameters measurements were more difficult to collect and therefore determined to be less reliable than the height measurements. Direct measures of age (tree ring counts) were not conducted, in order to minimise the damage to *P. alpinus* individuals, and because *P. alpinus* lack pronounced year-to-year variability in ring width which makes dating this species difficult (Dunwiddie 1979).

The mean percent foliage cover was then calculated from the survival percentage for “Damaged” individuals. This survival percentage from the “Damaged” individuals was also used to calculate the rate of foliar recovery using the formula:

$$\frac{\text{mean percent foliar recovery}}{4.5}$$

4.5

The number 4.5 was used in the above formula as the majority of sampling occurred 4.5 years after the August eruptions, and would therefore produce a rate of foliar recovery per year. This is assuming all individuals started with no foliage and that foliar recovery is linear.

2.3 Statistical analysis

To determine if the observed correlation between life state and distance from the eruption (Upper Te Maari) was statistically significant, a quadratic regression was conducted on IBM SPSS Statistics (2017). A linear regression was also performed on IBM SPSS Statistics (2017) to ascertain if the growth form of *P. alpinus* had a statistically significant correlation with the number of “Damaged” individuals. These types of regression were the best fit for each data set.

Non-metric multidimensional scaling (NMDS) ordinations in the ‘vegan’ package in R (Oksanen et al. 2015) were used to explore differences in the survival state of *P. alpinus*. Two approaches were used to investigate the survival states which could be either “Dead”, “Live”, or “Damaged”. The first approach entailed an ordination where population structures were formed by the number of “Dead”, “Live”, or “Damaged” *P. alpinus* occurring in each plot. Clustering was then determined using the ‘vegdist’ function in the ‘vegan’ package to create a Bray Curtis dissimilarity matrix followed by clustering into three group averages. The second approach investigated survival by life state and height. The nine height categories (1-50 cm, 51-100 cm, 101-150 cm, 151-200 cm, 201-250 cm, 251-300 cm, 301-350 cm, 351-400 cm and 400+ cm), were also used for histograms of population structure. This second approach required three ordinations, one for each survival state: A) Dead *P. alpinus* (# individuals/hgt. category), B) Live *P. alpinus* (#individuals/hgt. category) and C) Damaged *P. alpinus* (# individuals/hgt. category). Prior to fitting all the ordination models, individual abundance data were square root transformed and standardized using a Wisconsin double relativization (Gauch 1982). The variables altitude, plot area, distance from eruption, tree height, slope, and aspect were log transformed and appeared as vectors on the NMDS plots if they were significantly correlated with the ordination axes ($\alpha = 0.05$).

2.4 Results

From the 660 *P. alpinus* individuals in this study, 278 were “Live”, 182 “Damaged” and 200 “Dead”. To investigate the survival of *P. alpinus*, at a plot level the proportion of individuals in each life state were visually represented (Figure 2.10). The trend from this visual representation appears to show that the closer the plots are to the source of the eruption (Upper Te Maari), the more likely *P. alpinus* is to

be “Dead”, while the further *P. alpinus* is from Te Maari, the more likely it is to be “Live”.

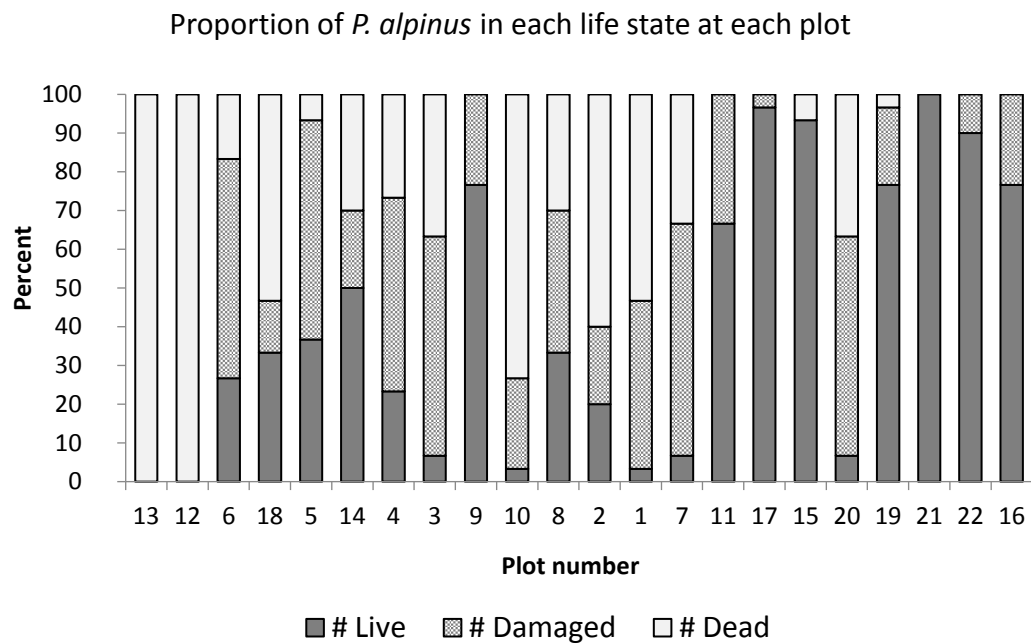


Figure 2.10 Proportion of each life status (“Live”, “Damaged” and “Dead”) at each plot. Plots are in order of distance from the eruption, with Plot 13 the closest.

To determine if this trend was statistically significant at a $P < 0.05$ level, a quadratic regression was conducted. The regression showed the number of “Live” and “Dead” *P. alpinus* per plot were correlated to the distance from the eruption (Figure 2.11). Plots close to the eruption had a higher number of “Dead” *P. alpinus* while those plots on the outer limits of the eruption zone had a higher number of “Live” *P. alpinus*. The number of *P. alpinus* “Damaged” at each plot did not show a significant correlation with distance to the eruption.

Number of *P. alpinus* “Live”, “Dead” and “Damaged” within each plot

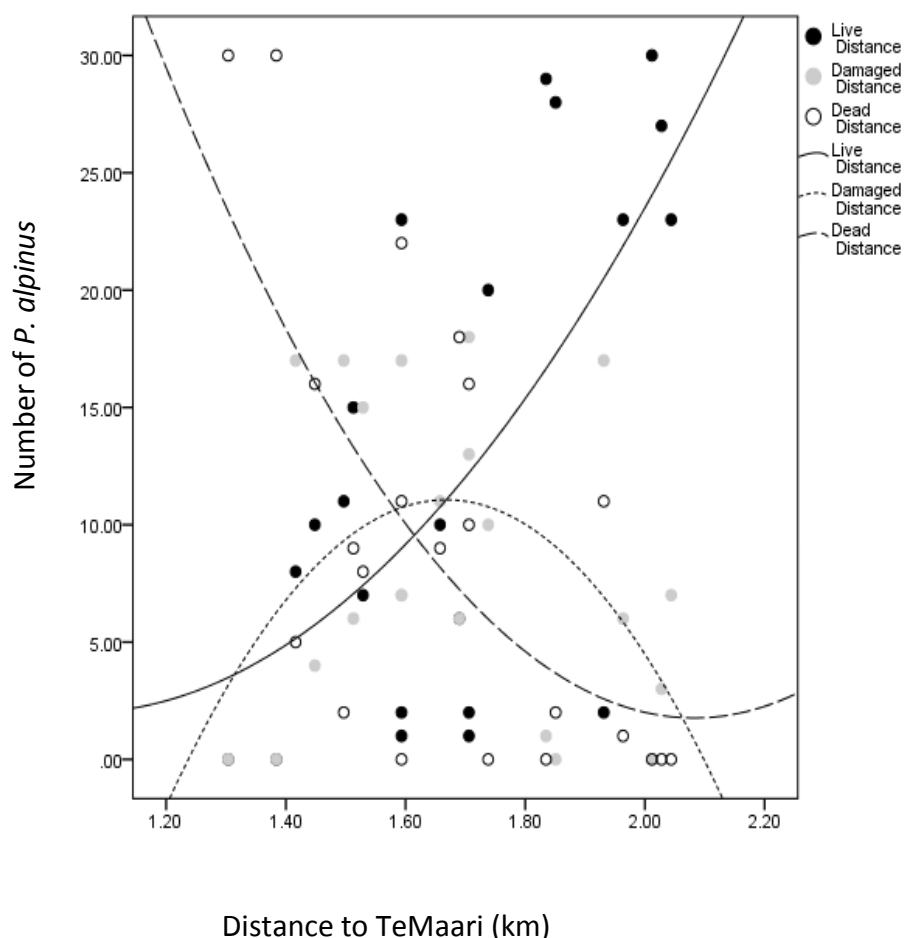


Figure 2.11 Quadratic Regression of “Live” ($R^2 = 0.418$, 21 d.f, $P = 0.006$), “Dead” ($R^2 = 0.424$, 21 d.f, $P = 0.005$) and “Damaged” ($R^2 = 0.201$, 21 d.f, $P = 0.118$) *P. alpinus* per plot, with respect to their distance from the eruption source (Upper Te Maari).

A NMDS ordination was then conducted to ascertain if distance to the eruption was the only variable significantly correlated to the life state of *P. alpinus* (Figure 2.12).

The results showed:

1. Altitude is significantly correlated with plots that are “Damaged”, with the raw data indicating as altitude increases the likelihood of *P. alpinus* being “Damaged” also increases.
2. Plot area is correlated with plots classified as “Live” and “Damaged”, with the strongest correlation towards the “Live” plots. The raw data illustrates as plot area increases the number of “Live” and “Damaged” *P. alpinus* also increases.

P. alpinus population structures

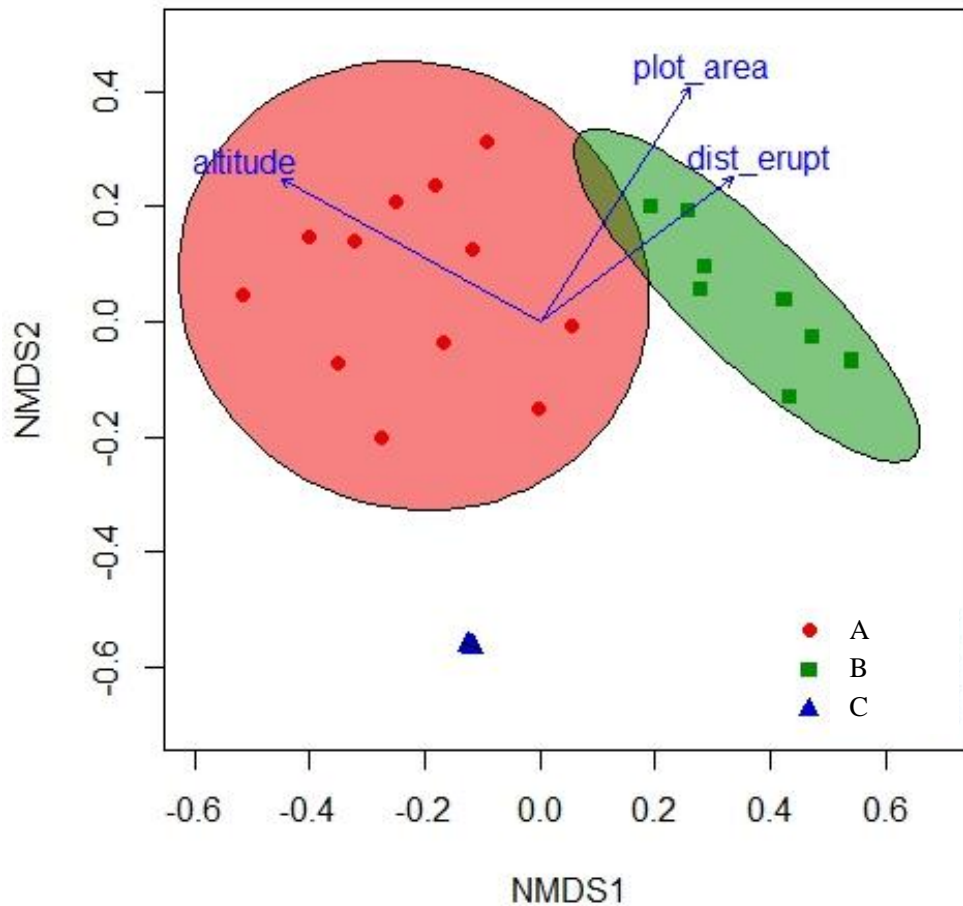


Figure 2.12 An NMDS ordination graph illustrating population structures by life status (numbers of “Live”, “Dead” and “Damaged” *P. alpinus*). Points on the graph represent individual research plots, with overlaid, shaded ellipses denoting clustering of plots most similar to each other. Clusters represent plots which are proportionally A) “Damaged” B) “Live” and C) “Dead”. Ellipses are formed based on cluster means and standard deviations. Vectors illustrate directions of significant environmental variables ($\alpha = 0.05$), length of arrow is proportional to its correlation with the ordination. Final NMDS stress was 0.0600.

There was no significant correlation with plots classified as “Dead”. The position of these plots within the research area and their associated clusters are shown in Figure 2.13.

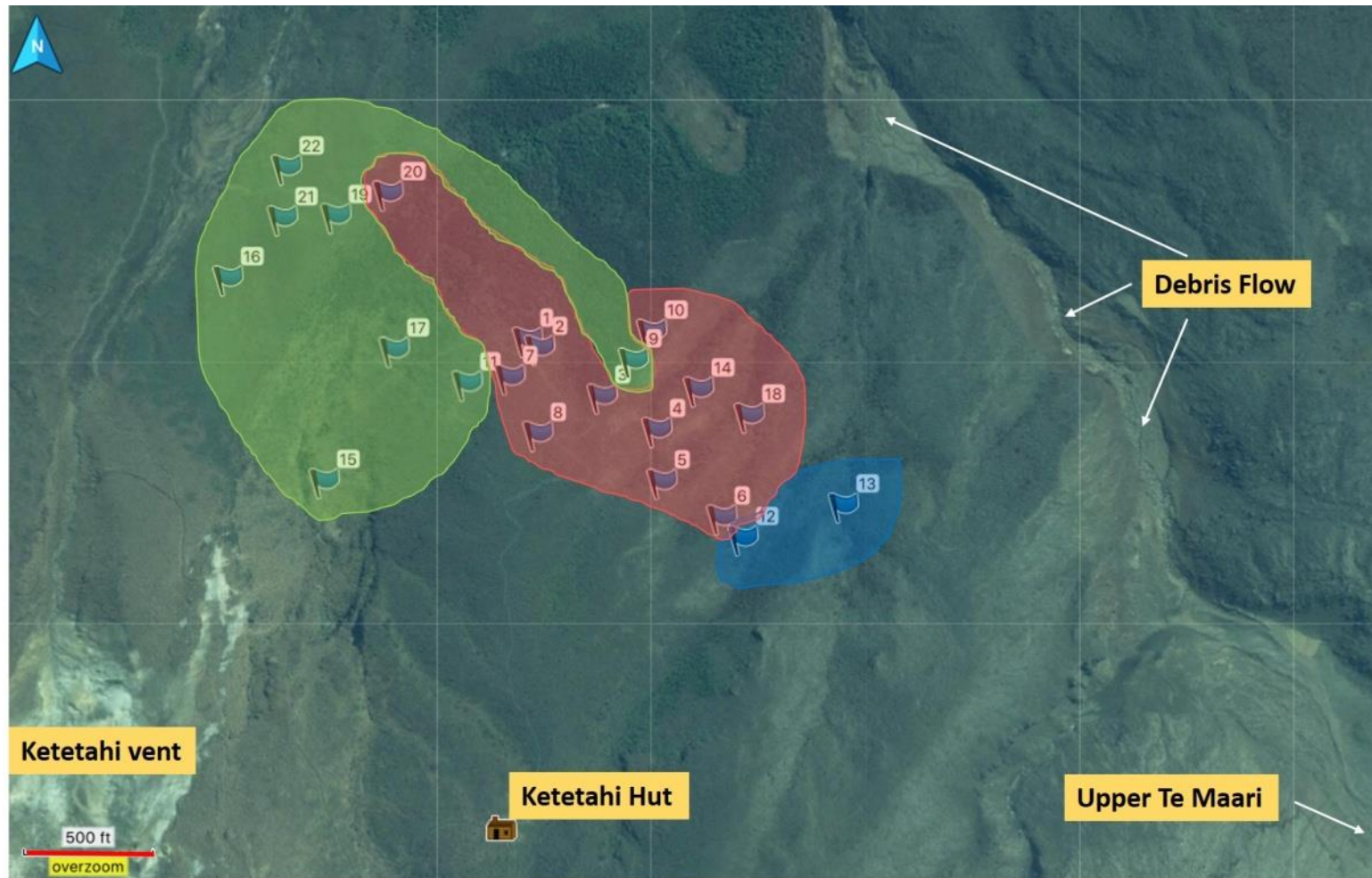


Figure 2.13 Plot locations, overlaid with their NMDS classifications from Figure 2.12

To examine if the age of *P. alpinus* affected the survival, a population structure of the 660 *P. alpinus* sampled within the eruption zone, was created using height classes (Figure 2.14). The population structure showed that height classes below 250 cm contained individuals in all three life states, however very few individuals above 250 cm are “Damaged” and individuals between 0 and 50 cm are predominantly “Live” or “Damaged”.

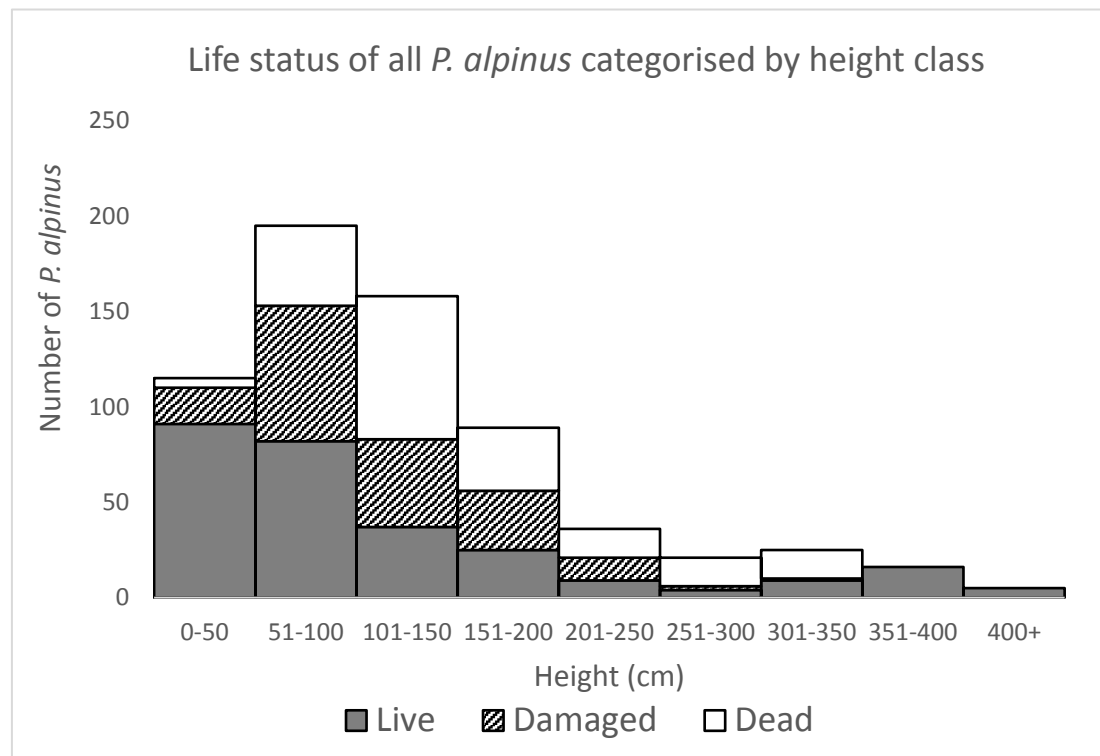


Figure 2.14 Life states of all *P. alpinus* sampled within the eruption zone.

This suggests age may affect the survival of *P. alpinus*, particularly “Damaged” individuals. To examine this further, population structures for all plots were created, which showed a wide range of population structures exist within the eruption zone. Plots were then placed into their cluster of “Live”, “Dead” or “Damaged” as identified in Figure 2.12, with representative population structures for each cluster illustrated below (Figure 2.15).

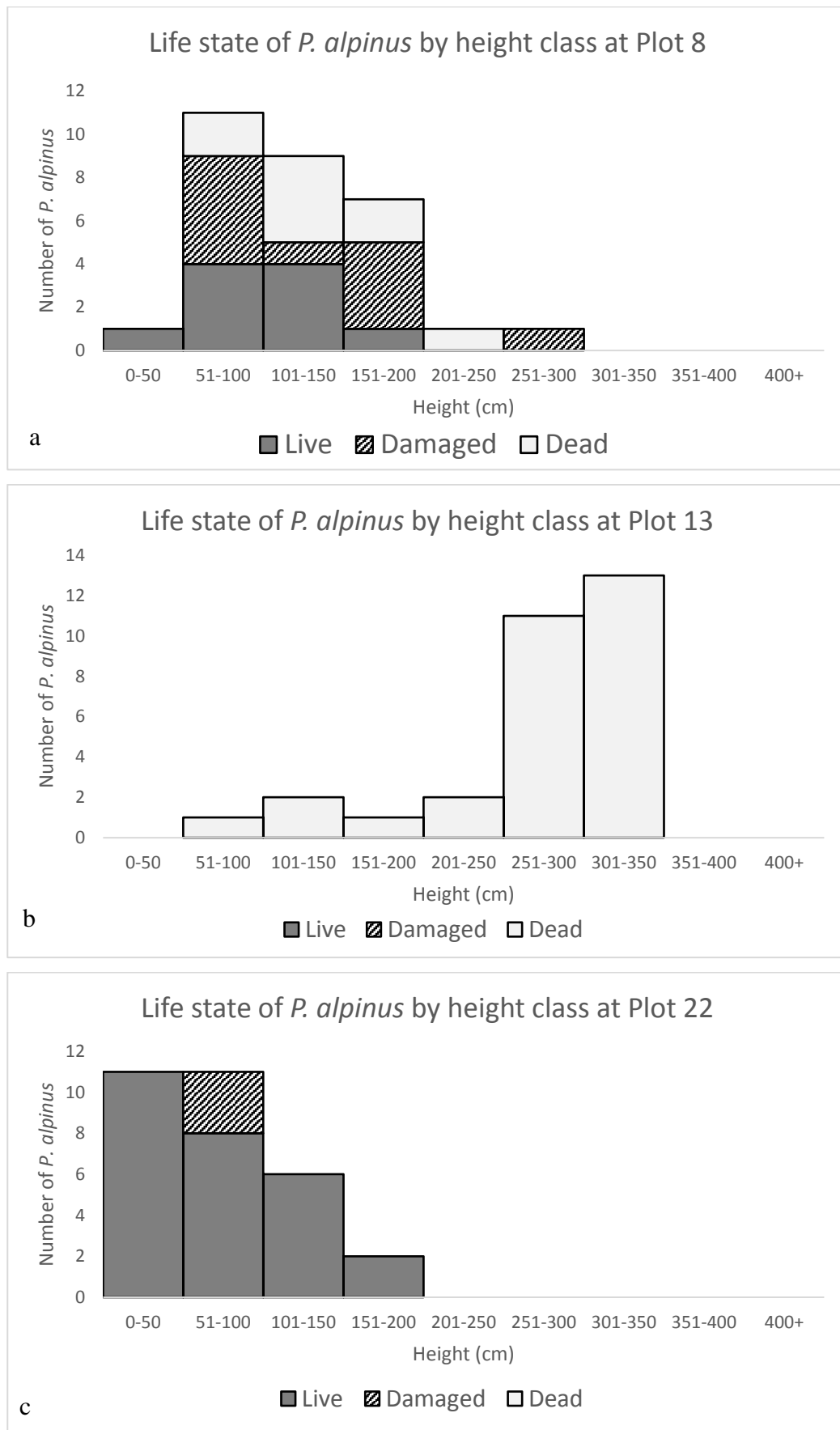


Figure 2.15 Population structures representative of the variation in *P. alpinus* at a plot level. a) Plot 8, is representative of the “Damaged” cluster of Figure 2.12; b) Plot 13, is representative the “Dead” cluster of Figure 2.12; c) Plot 22, is representative of an “Live” cluster in Figure 2.12.

Based on the population structures, it appeared age did effect the survival of *P. alpinus*, with Figure 2.15b showing a deceased mature population and Figure 2.15c showing a predominantly young alive population. To determine if this was statistically significant an NMDS ordination was constructed using population structures by life state (A = “Dead”, B = “Live” and C = “Damaged”) and height classes (Figure 2.16). The results showed:

- A. Tree height is significantly correlated with plots containing “Dead” *P. alpinus*, with the raw data indicating taller (and therefore older) *P. alpinus* are more likely to be “Dead”. This ordination also showed both distance to the eruption source and plot area are significantly correlated with “Dead” *P. alpinus*. The raw data illustrated that as density and distance to the eruption increased, the likelihood of *P. alpinus* being “Dead” also increases.
- B. Tree height is significantly correlated with plots containing “Live” *P. alpinus*, with the raw data indicating smaller (and therefore younger) *P. alpinus* are more likely to be “Live”.
- C. Altitude is significantly correlated with “Damaged” *P. alpinus*, with the raw data illustrating as altitude increases the likelihood of *P. alpinus* being “Damaged” also increases.

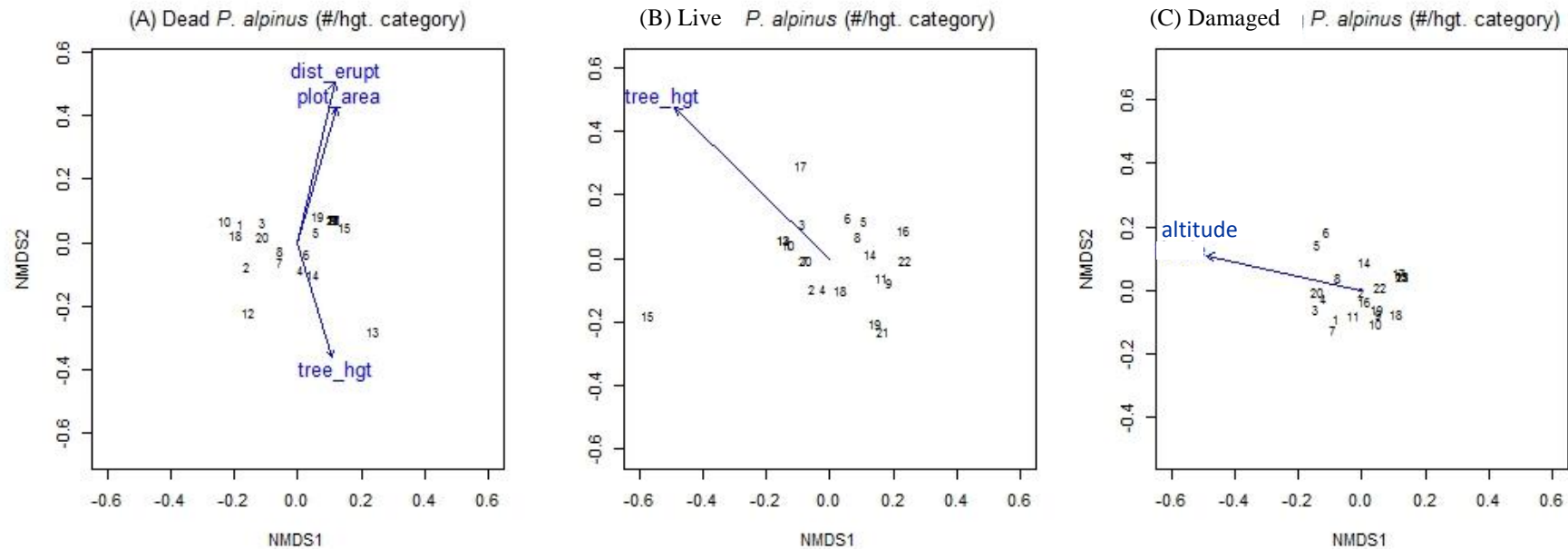


Figure 2.16 NMDS ordination plots illustrating population structures by life status and height categories: A) “Dead” *P. alpinus* (# individuals/hgt. category), B) “Live” *P. alpinus* (#individuals/hgt. category) and C) “Damaged” *P. alpinus* (# individuals/hgt. category). Numbers on graphs represent individual research plots. Plots situated within close proximity reflect similar population structures by life statuses. Vectors illustrate directions of significant environmental variables ($\alpha = 0.05$), length of arrow is proportional to its correlation with the ordination. Final NMDS stresses were A) 0.1014, B) 0.0708 and C) 0.1725.

As the number of “Damaged” *P. alpinus* was significantly correlated with altitude, a linear regression was performed to determine if the growth form of *P. alpinus* could be attributed to this correlation (Figure 2.17). This regression included individuals from all life states, not only the “Damaged” *P. alpinus* category, as the growth form (tree or shrub) would have developed before the PDCs effected individuals (with the exception of new juveniles). Including all individuals gives a larger sample size, and results that are more precise. The results showed the number of single stemmed *P. alpinus* increased as altitude increased, and the number of multi-stemmed *P. alpinus* decreased when altitude increased. This was statistically significant at a $P < 0.1$ level, not at a $P < 0.05$ level ($P = 0.056$).

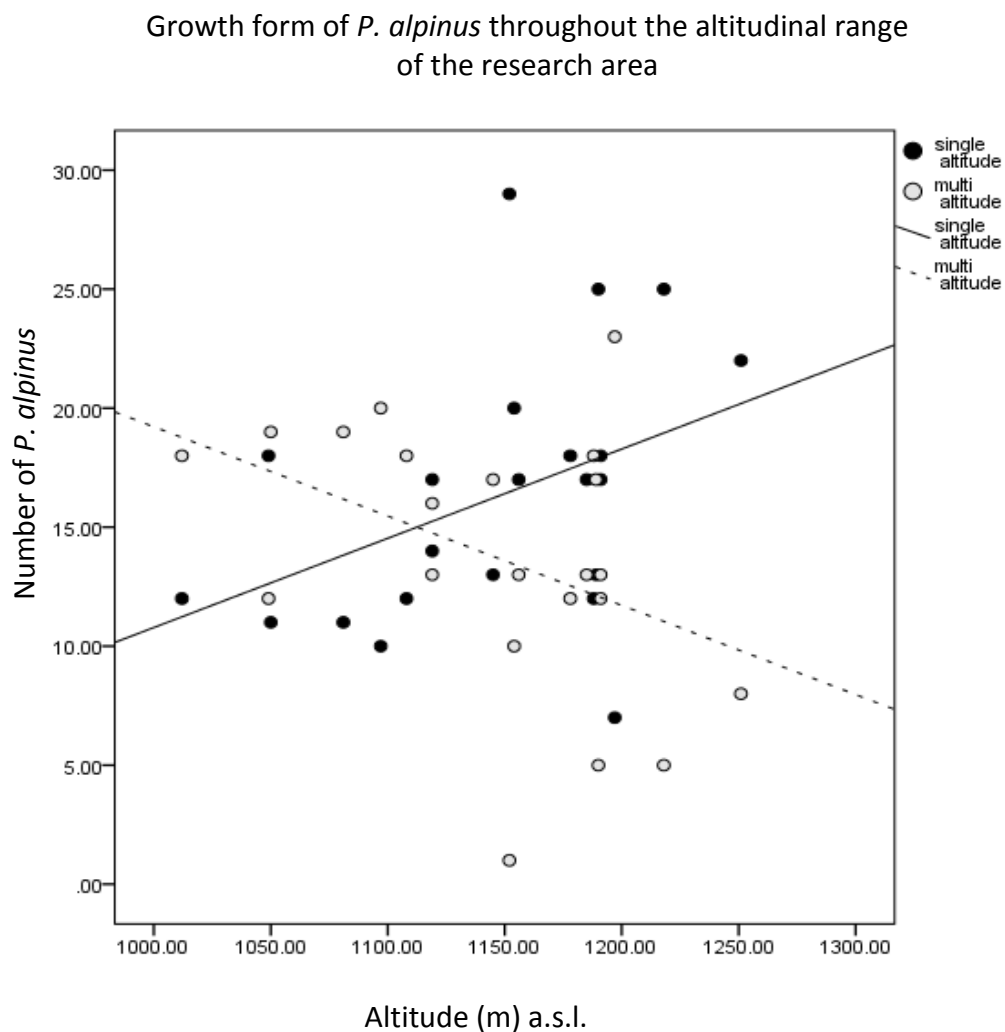


Figure 2.17 Linear regression showing the number of single stemmed ($R^2 = 0.171$, 21 d.f., $P = 0.056$) and multi-stemmed ($R^2 = 0.171$, 21 d.f., $P = 0.056$) *P. alpinus* throughout the altitudinal gradient of the research area.

To determine the rate of foliar recovery for “Damaged” *P. alpinus*, and if age affected this rate, data was examined by height class. The mean foliage cover for height classes below 251 cm was 76.14%, ranging from 75.13% - 76.98% (Figure 2.18). This shows that the rate of foliar recovery is not affected by the height (and therefore age) of the individual.

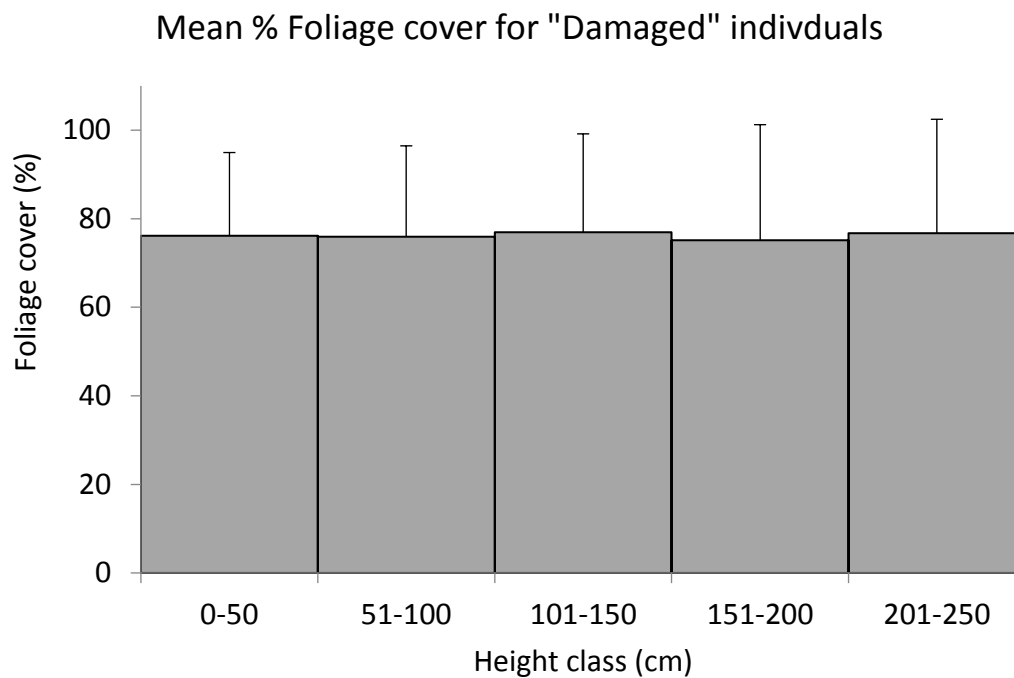


Figure 2.18 Mean foliar cover for by height class for all individuals classified as “Damaged”. The number of individuals per height class are: n=19 (0-50 cm), n=69 (51-100 cm), n=46 (101-150 cm), n=29 (151-200 cm), n=11 (201–250 cm). Height classes above 251 cm were excluded due to a lack of “Damaged” individuals in each height class (n<3).

The overall mean percent foliage cover for all “Damaged” individuals is 75.59%. As the mean time for the data collection occurred 4.5 years after the eruption, the rate of foliar recovery is 16.80 % per year; assuming all individuals started with no foliage and that foliar recovery is linear.

2.5 Discussion

2.5.1 Survival of *P. alpinus* within the eruption zone

Although from observation there was widespread canopy die back of *P. alpinus* throughout the eruption zone, of the 660 individuals in this study, 278 were “Live”, 182 were “Damaged” and only 200 were “Dead”. The number of “Live” and “Dead” *P. alpinus* varied throughout the affected area. Those plots closer to the eruption contained significantly more “Dead” *P. alpinus* while those plots on the outer limits of the eruption zone contained significantly more “Live” *P. alpinus*. These correlations are likely the result of higher PDC temperatures near Te Maari. Efford et al. (2014) described temperatures close to the eruption were probably $>64^{\circ}\text{C}$ while temperatures at the distal end of the eruption zone (where more “Live” individuals were located), were probably between 51°C and 58°C . Efford et al. (2014) recreated these temperatures in a water bath and found the percent of foliage browning for *P. alpinus* between 50°C and 66°C was dependant on the time of exposure to these temperatures. At a temperature of 60°C and a duration of 30 seconds, 40% of *P. alpinus* foliage browned. At the same 60°C temperature, for 120 seconds duration, 100% of the foliage was browned.

The estimated duration of the PDC during the eruption was 60 seconds. For *P. alpinus*, at 60 seconds. 0% foliage browning occurred at 50°C or below while 100% foliage browning occurred at 58°C or higher. As the PDCs closest to Te Maari were $>64^{\circ}\text{C}$, this would correlate with the 100% browned foliage seen above 58°C , and therefore potentially a higher incidence of “Dead” *P. alpinus*, with proximity to the eruption source. Between temperatures of 50°C and 58°C , for a duration of 60 seconds, the percent of foliage browning varied. At 51°C - 53°C approximately 20% of the foliage browned, at 54°C approximately 40% of the foliage browned, at 55°C approximately 60% of leaves browned and at 56°C – 57°C , 80% of these leaves browned. The temperatures at the distal end of the eruption zone were expected to be between 51°C and 58°C (assuming a gradual decrease in temperature with distance from Te Maari), which correlates with the decrease in foliage browning and possibly a higher incidence of *P. alpinus* being “Live” with distance from Te Maari.

Although there was no correlation for the number of “Damaged” *P. alpinus* with distance to Te Maari, the first NMDS ordination (Figure 2.12) showed there was a significant correlation with altitude. The raw data indicated as altitude increased, the number of “Damaged” *P. alpinus* also increased. This information combined with the quadratic regression suggests plots in the centre of the research area (where “Damaged” individuals are most prevalent) are at higher altitudes than plots close to the eruption source or at the distal end of the eruption zone. Examination of the raw data shows plots between the centre of the research area and close to Te Maari had the highest altitudes. As “Damaged” individuals displayed some green foliage (either existing and/or resprouted), there could be one of two scenarios to explain this outcome. Firstly, perhaps the exposure to the PDCs was more intense further down the mountain due to its path, the topography of the terrain, and the heights of individuals (which are discussed further in section 2.5.2) They may have resulted in minimal damage to individuals at high altitudes rather than causing death. Secondly, more individuals at higher altitudes are resprouting compared to those at lower altitudes.

After disturbance, shrubs (multi-stemmed) have a greater area for sprouting compared with trees (single stemmed) (Götmark et al. 2016). As *P. alpinus* can be either a tree or a shrub, a linear regression was performed to determine if this increase in “Damaged” individuals with altitude could be attributed to the growth form of *P. alpinus*. The regression showed the growth form of *P. alpinus* did change with altitude. The number of single stemmed *P. alpinus* increased as altitude increased, and the number of multi-stemmed *P. alpinus* decreased when altitude increased. This was statistically significant at a $P < 0.1$ level but not at a $P < 0.05$ level ($P = 0.056$). These results are contrary to the expected results. Usually “along an altitudinal gradient the tree growth form gives way to the shrub growth form. So at higher altitude there are more climatic stresses and the multiple leader growth form will be more common” (B Clarkson 2017 Pers. Comm., 3 Oct). One possible explanation for the increase of single stemmed trees is that an increase in altitude is associated with an increase in wind exposure. To provide strong anchorage against this wind, many alpine plants develop a deep root structure (Otago Conservancy 2005). Although conifers like *P. alpinus* tend to have shallow, wide-spreading root systems for anchorage (Dawson et al. 2011), trees tend to develop deeper root systems than shrubs (Schenk & Jackson 2002) and therefore could withstand the

increase in wind. A larger root system also means larger food reserves, which can be utilised when the demand arises (Glerum 1980), such as after disturbance when individuals require energy to produce new sprouts. A larger energy reserve could therefore lead to the increase in the number of individuals resprouting with the increase in altitude. Another and more probable explanation for the increase in single stemmed individuals at higher altitudes is the age of the mature stands. As stands mature and reach their carrying capacity, competition intensifies and self-thinning occurs (Li et al. 2000). In the research area, older, taller stands (of all life states) were often located close to Te Maari, in deep gullies and at mid-high altitudes. Before the PDCs affected these stands, the individuals in these areas may have received more protection from environmental stresses, compared to individuals in the more open areas at lower altitudes, and therefore enabled the development of more mature stands in these locations. The development of a more mature stand will result in higher numbers of trees rather than shrubs and therefore an increase in single stemmed individuals with altitude may be a reflection of the age of the stand rather than factors directly associated with altitudinal changes such as wind exposure.

Plot area was also significantly correlated with plots classified as “Live” and “Damaged” in the first NMDS ordination (Figure 2.12), with the strongest correlation towards the “Live” plots. The raw data showed as plot area increased the number of “Live” and “Damaged” *P. alpinus* increased. As each plot contained 30 individuals, plot area is a direct reflection of density, the larger the plot area the less dense the population of *P. alpinus* within the plot. The results can therefore be interpreted as showing when the density of *P. alpinus* decreases the number of “Live” and “Damaged” *P. alpinus* increases. Surprisingly this suggests individuals which were not sheltered by other individuals had a higher rate of survival and/or resprout. Examining the plots and data collected, it appears the plots which had that largest areas were often located further from Te Maari. From the quadratic regression (Figure 2.11) we know the number of “Live” *P. alpinus* significantly increased with distance from the Te Maari, which was most likely associated with lower PDC temperatures during the eruption. A correlation between plot area and the number of “Live” *P. alpinus* may therefore be due to the location of the plots rather than factors associated with density directly.

The number of “Damaged” individuals however was not correlated with the distance to Te Maari, therefore the locations of the plots with respect to Te Maari does not reflect the number of “Damaged” individuals increasing with plot size. There was a significant correlation with the number of “Damaged” individuals and altitude. If larger plots were associated with higher altitudes this may explain the number of “Damaged” individuals increasing, however examination of the raw data showed no association of plot size with altitude. The number of “Damaged” individuals are therefore directly correlated to the area of the plot. As *P. alpinus* is one of the taller species in the landscape, lower density means individuals will have more light availability and therefore more energy produced via photosynthesis to create new sprouts. As “Damaged” individuals displayed some green foliage (either existing and/or resprouted), this could reflect more individuals resprouting with increased light availability from increasing plot area.

The NMS based on the population structures and clusters (Figure 2.12), does not directly show a significant correlation with plots classified as “Dead”, unlike the results displayed in the quadratic regression (Figure 2.11). This is most likely due to the type of analysis. An NMDS can only plot a vector in one direction. The NMDS is placing plots in a 3-dimensional space based on the data given, and plots the strongest correlation. Only two of the 22 plots showed extremely high levels of death, while eight plots had large numbers of “Live” individuals. The “Live” plots were most likely the strongest correlation based on the data, therefore the vector is showing the significance in that direction. Based on this and the results of the quadratic regression (Figure 2.11), it can still be concluded that distance to the eruption affects the number of “Live” and “Dead” *P. alpinus*, with individuals closest to the eruption source more likely to be “Dead”.

2.5.2 Influence of age on *P. alpinus* survival

To ascertain if the age of *P. alpinus* influenced survival, further NMDS ordinations for those individuals “Live”, “Dead” and “Damaged” were performed using population structures by height class (Figure 2.16). Ordination (A) showed tree height significantly correlated with plots containing “Dead” *P. alpinus*, with the raw data indicating taller *P. alpinus* (and therefore older individuals) are more likely to be “Dead”. Ordination (B) showed tree height was significantly correlated with plots containing “Live” *P. alpinus*, with the raw data indicating smaller *P. alpinus*

(and therefore younger individuals) are more likely to be “Live”. As PDCs can move uphill and “jump” over ridges (Dale et al. 2005) these results could be attributed to the topography on Mt Tongariro, particularly the slope and position of the ridges. As the PDC was estimated to be initially travelling between 55 - 115 m/s, the windward side of a steep ridge may have acted as a “ramp”, in which the PDC may have travelled over the top of the ridge and not immediately touched the ground on the leeward side. In this instance, the taller and older the individual is, the higher the chance it will be in the path of the PDC, especially on the leeward side of the ridge. This would therefore increase the chance of taller, older *P. alpinus* being affected by the PDC. This view of taller vegetation being more likely to be affected by PDCs is supported by del Moral and Grishin (1999) who stated that “pyroclastic events will most severely impact taller vegetation”.

Distance to the eruption was also shown to be significantly correlated with “Dead” *P. alpinus* in the second NMDS ordination (Figure 2.16a). This supports the results of the quadratic regression which showed the number of “Dead” *P. alpinus* increased with proximity to the eruption source, however this NMDS result suggests those “Dead” *P. alpinus* close to the eruption are the older individuals within the population. As discussed previously, this high death rate is most likely due to the temperature and exposure of the PDC’s close to the eruption source.

Plot area was also significantly correlated with “Dead” *P. alpinus* in Figure 2.16a, suggesting older *P. alpinus* individuals were located in close proximity to each other. Smaller plots containing older, “Dead” *P. alpinus* were often located close to Te Maari. This correlation between plot area and the number of “Dead” *P. alpinus* is most likely due to the location of the plots sampled, the temperatures of the PDCs, and prior limited disturbance allowing more mature stands to develop in those locations.

“Damaged” *P. alpinus* in Figure 2.16c show a significant correlation with altitude, however, tree height does not show a significant correlation with “Damaged” individuals. This suggests “Damaged” individuals are not associated with a specific age (further discussed in section 2.5.3). The correlation between “Damaged” individuals and altitude is reflected in the initial NMDS (Figure 2.12), and as discussed earlier, this could be attributed to either the path of the PDC or an increase

in light availability; although plot area (and therefore light availability) was not significantly correlated with “Damaged” in this ordination

2.5.3 Age and of “Damaged” *P. alpinus*.

The mean percent foliage cover for the 182 “Damaged” individuals is 75.59%. As shown in Figure 2.18, the age of “Damaged” *P. alpinus* does not significantly affect this foliage cover.

As the mean time for the data collection occurred 4.5 years after the August eruptions, the rate of foliar recovery is 16.80% per year. This is assuming all individuals started with no live foliage and that the recovery rate is linear. Although “Damaged” individuals by definition could have already possessed foliage prior to the eruptions, the extent of this unknown, and therefore could not be included in the foliar recovery calculation. Based on the foliar recovery, *P. alpinus* is projected to fully recover within 6 years of the eruptions. Examination of other species in the vicinity, from 2013 - 2017, suggest recovery is not a linear process however. Caccianiga et al. (2006) also suggest alpine plant growth is not continuous, as they experience seasonal snow cover and/or frozen soil which can inhibit plant growth. This projection should therefore be viewed with caution.

2.6 Summary and Recommendations

The survival of *Phyllocladus alpinus* varies within the eruption zone. “Dead” *P. alpinus* tend to be older, taller individuals, in close proximity to each other, and located close to Te Maari. “Live” *P. alpinus* show the opposite trend, they tend to be younger, shorter individuals, who are located further apart and at the distal end of the eruption zone. The number “Live” and “Dead” individuals is most likely due to the temperatures associated with, and the level of exposure to, the PDC. “Damaged” individuals have on average 75.59% total foliage cover, which does not significantly change with age. The majority of “Damaged” individuals are located in large plots in the middle of the eruption zone, at mid-high altitudes. Increased light availability and the path of the PDC may contribute to the increase in “Damaged” individuals with plot size and altitude.

The findings of this study support del Moral and Grishin (1999), taller individuals are more likely to be severely affected by volcanic disturbance.

Ideally, this research would have occurred directly before and after the eruptions to establish a direct change in the species over time. Although the vegetation in this area was surveyed between 1960 and 1966, comparable data specific to the survival and growth of *P. alpinus* was not measured, and therefore direct comparisons to establish a change in this population as not possible. As precise data is unavailable it is assumed in the present study that no *P. alpinus* in the research area were “Dead” before the PDCs, and that all *P. alpinus* were “Live”.

Without a secondary data set to complement the data presented in this study, it is premature, at this point, to discuss successional pathways and which model of succession can best encompass the results. The preferred option is the data from the present study be used as a baseline with future measurements of this population used to examine secondary succession. In the future it would be beneficial to expand the current research and examine other factors which may affect the growth and survival of this population such as soil chemistry, texture and mycorrhizal associations which all conifers possess (Dawson et al. 2011). As volcanic sites tend to have limited nutrient availability (Dale et al. 2005), this mycorrhizal association may be not be a driving factor, however without scientific investigation the effect of this association is unknown.

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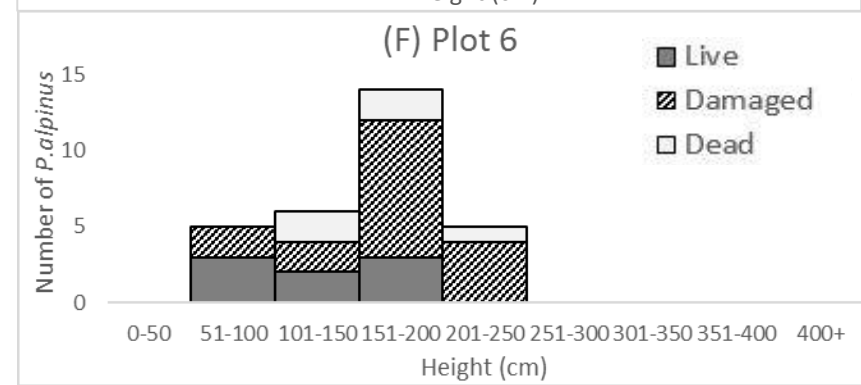
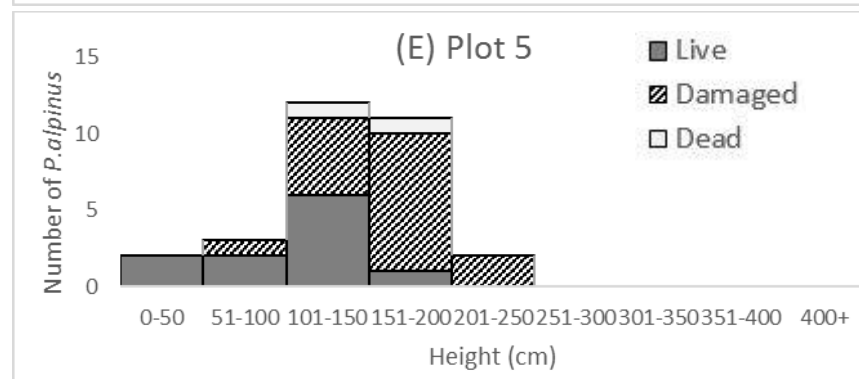
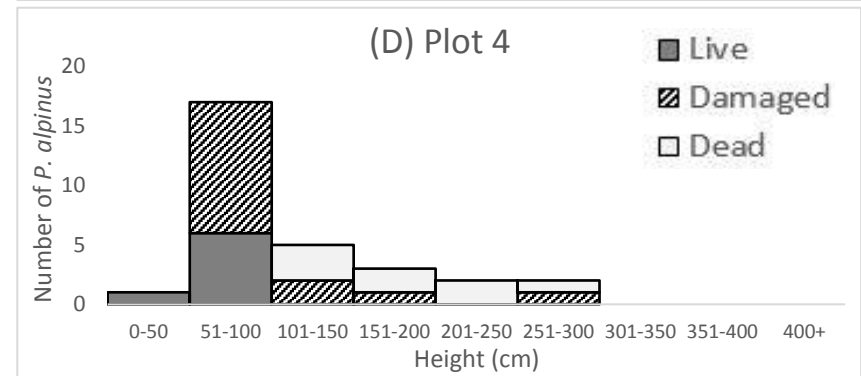
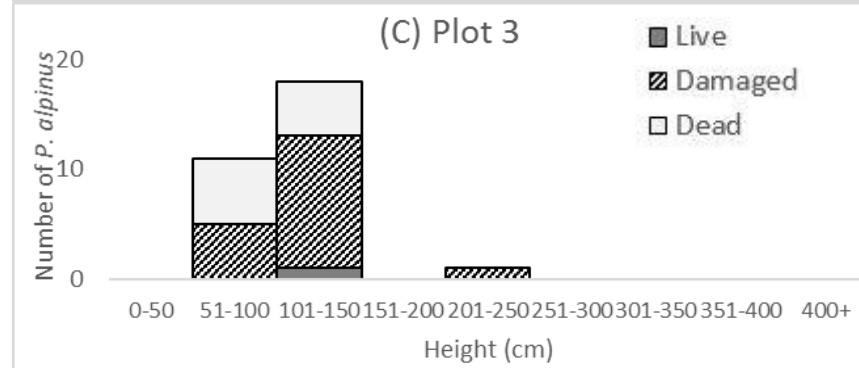
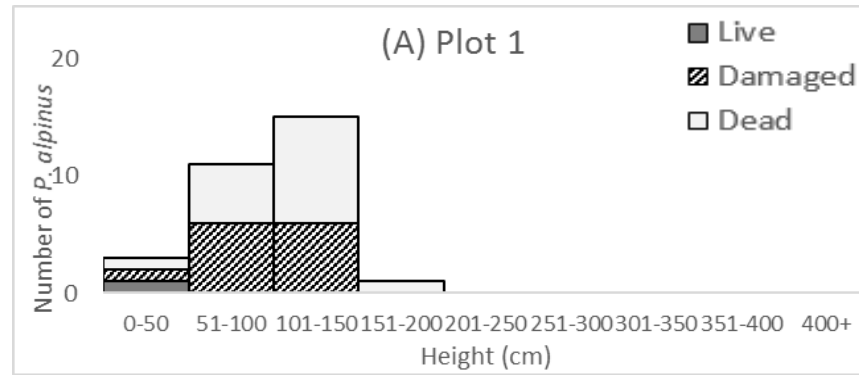
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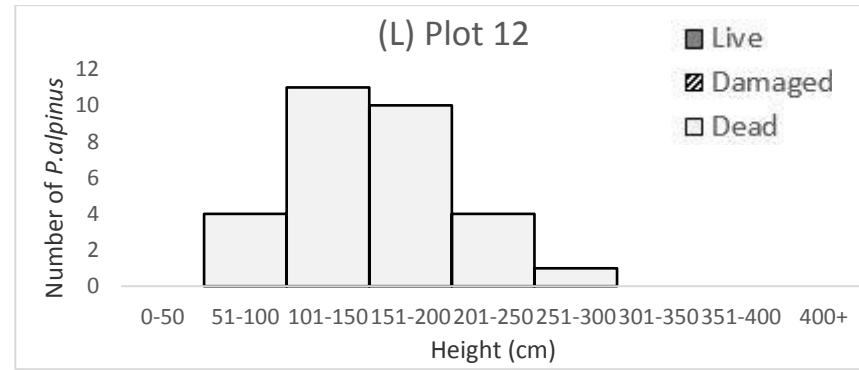
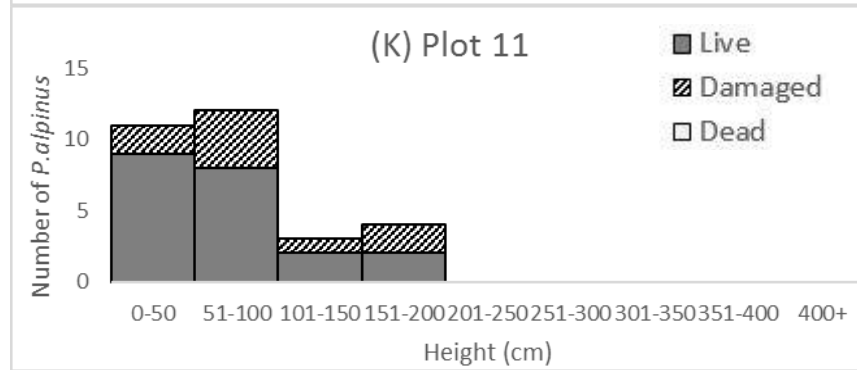
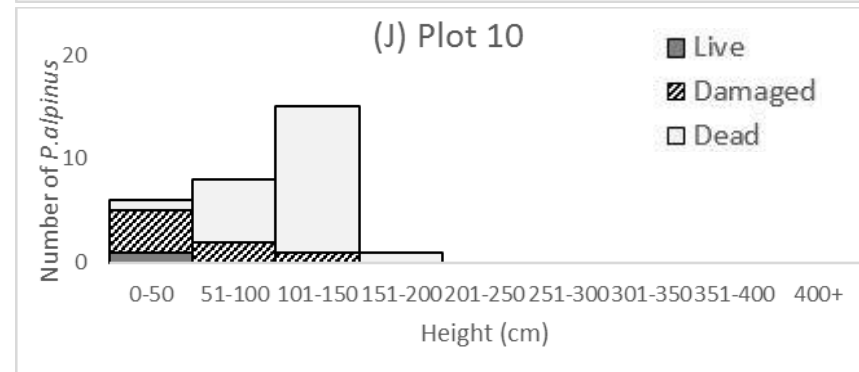
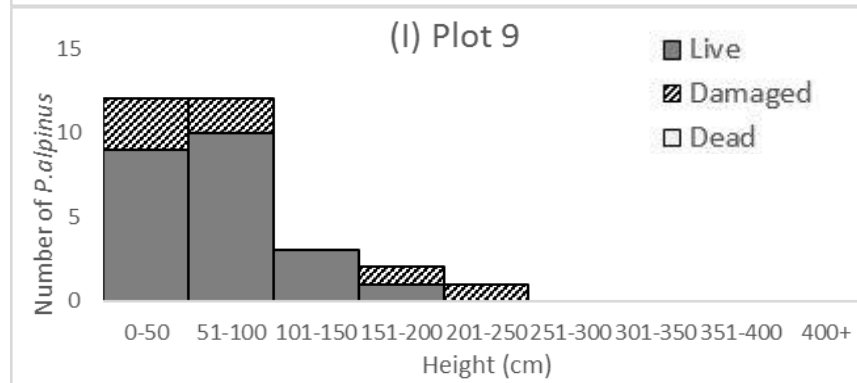
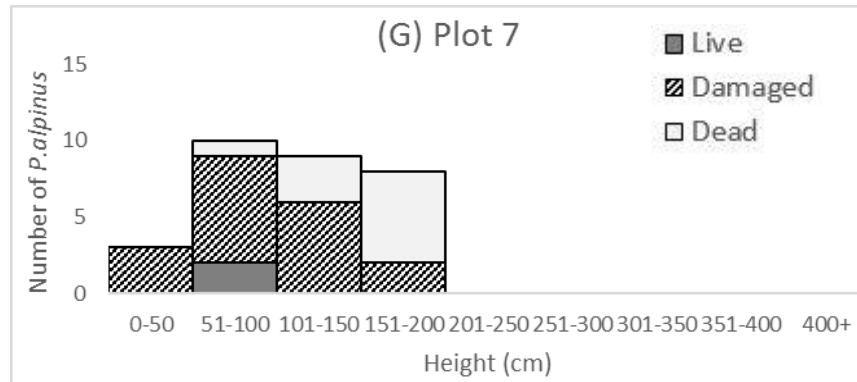
Appendices

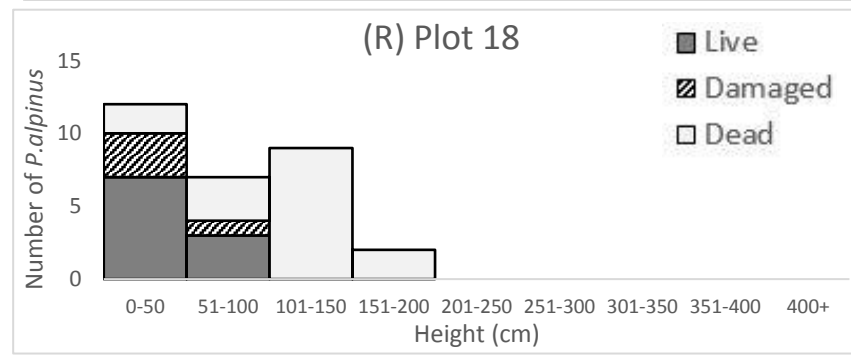
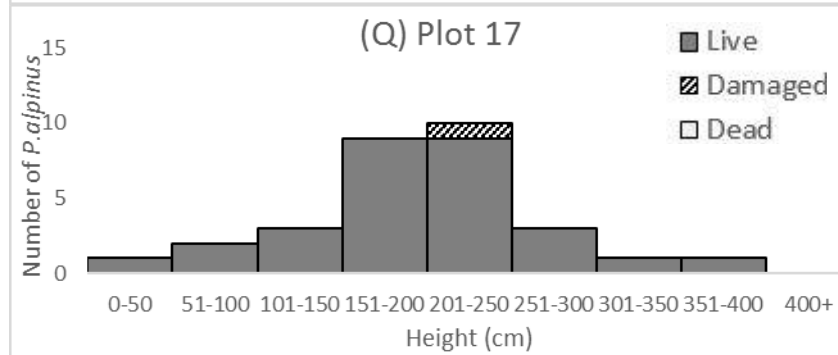
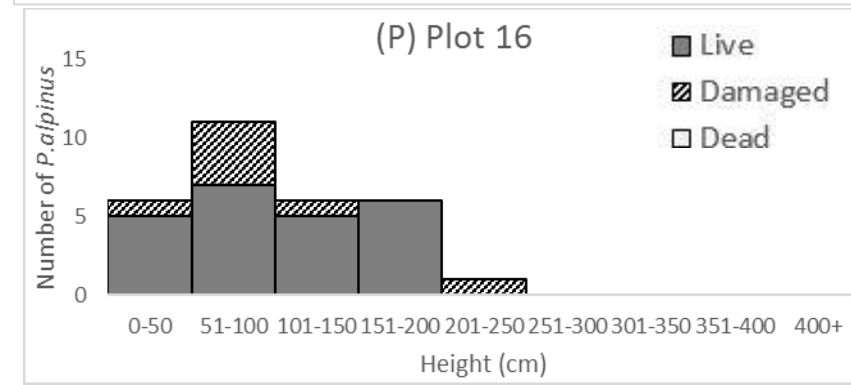
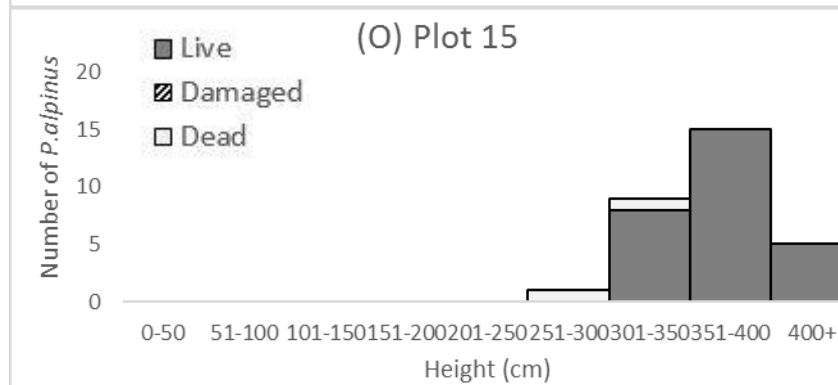
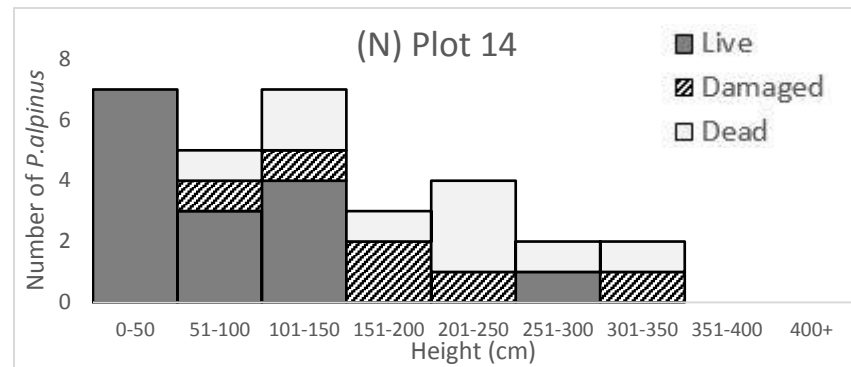
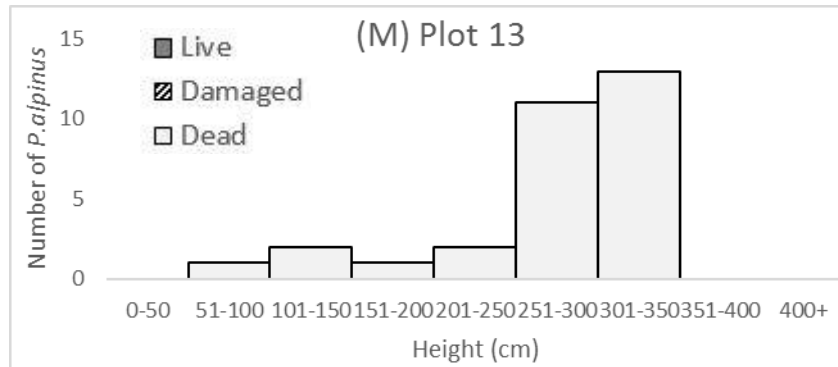
APPENDIX ONE

Table A1.1 Plot specific information relating to *P. alpinus* and species sensitivity data sets.

Plot ID	eastings	northings	Plot area (m ²)	Slope of plot (deg)	Altitude of plot (m)	Aspect of plot	Distance to Te Maari (km)
1	1829438	5668455	120.76	9	1191	N	1.705905
2	1829453	5668445	66.48	14	1178	N	1.689811
3	1829522	5668386	44.18	14	1190	NW	1.59325
4	1829580	5668345	124.69	24	1191	W	1.52888
5	1829583	5668286	139.35	20	1251	NW	1.49669
6	1829649	5668243	148.27	20	1218	NW	1.41622
7	1829419	5668411	193.59	22	1189	N	1.705905
8	1829448	5668342	175.30	22	1188	N	1.65762
9	1829556	5668427	103.51	22	1185	NW	1.59325
10	1829577	5668460	73.59	20	1197	W	1.59325
11	1829371	5668406	455.41	32	1154	NW	1.738092
12	1829672	5668217	58.63	29	1145	E	1.38404
13	1829784	5668252	14.39	5	1152	N	1.30357
14	1829627	5668392	84.95	16	1156	NW	1.51278
15	1829210	5668300	123.90	4	1097	N	1.85075
16	1829109	5668536	696.53	14	1119	NE	2.043867
17	1829291	5668448	485.39	28	1119	W	1.83465
18	1829683	5668363	122.72	15	1081	N	1.44841
19	1829231	5668605	87.25	29	1049	N	1.9634
20	1829289	5668630	82.35	34	1108	NE	1.93121
21	1829172	5668604	102.07	26	1050	W	2.01168
22	1829178	5668663	594.82	13	1012	N	2.027773







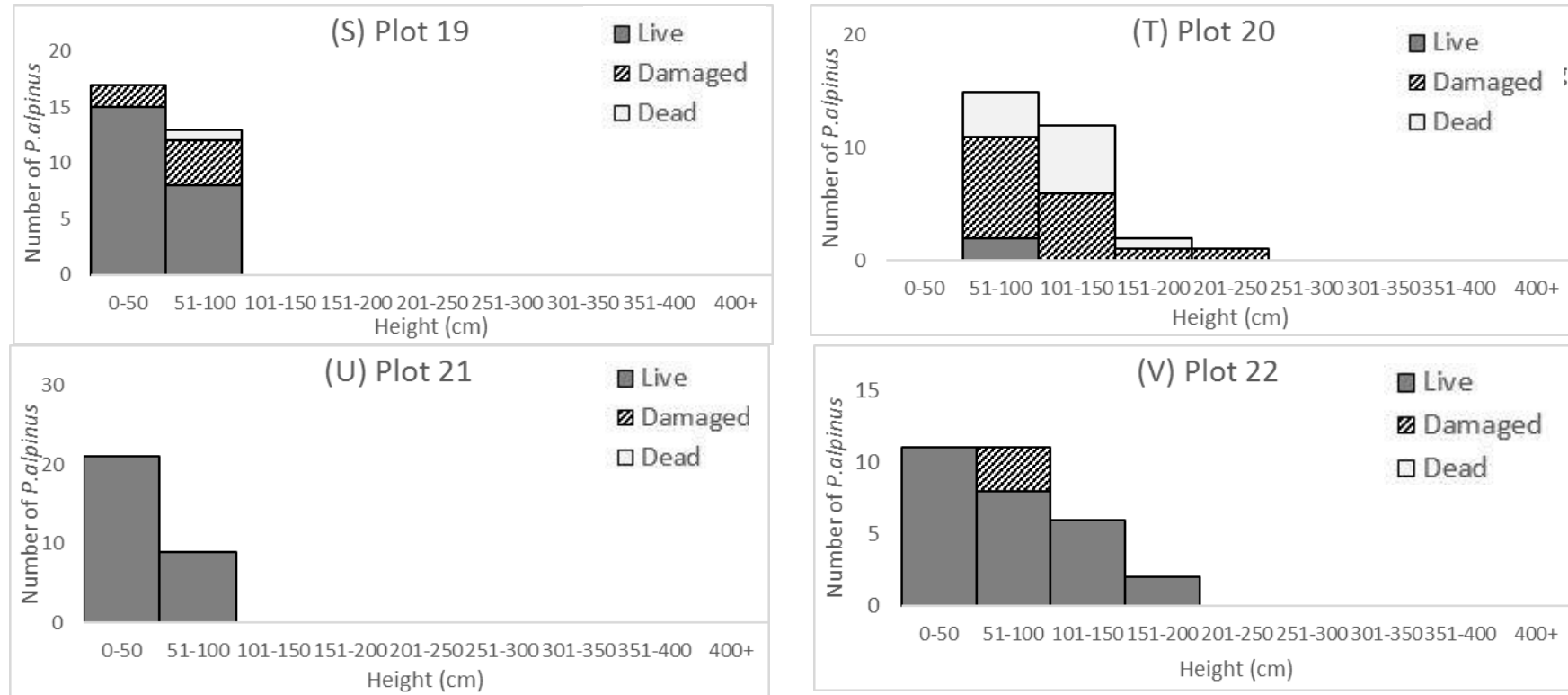
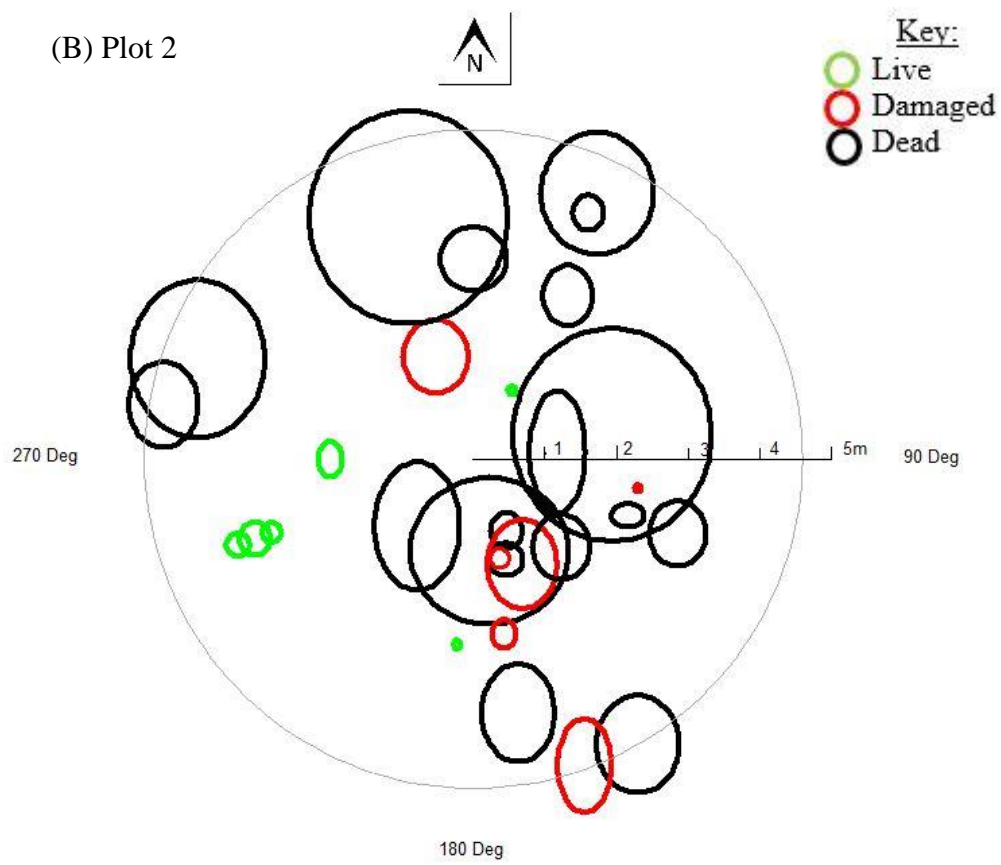
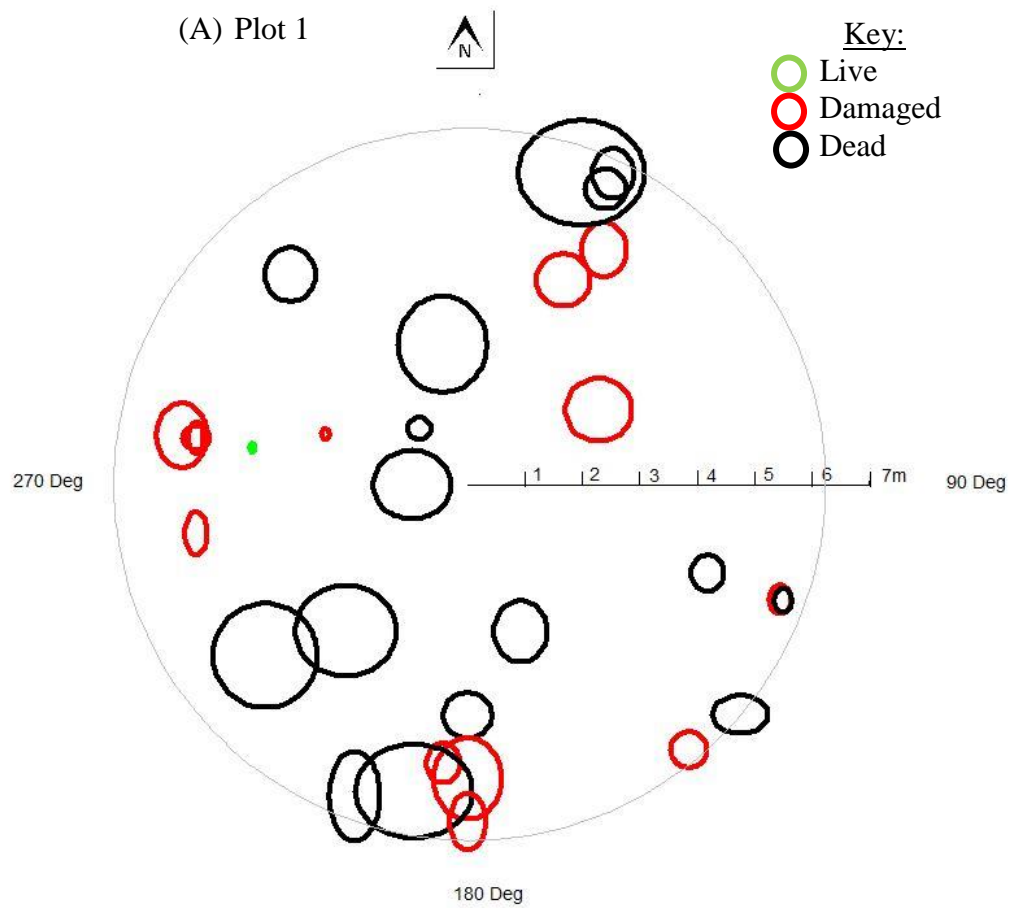
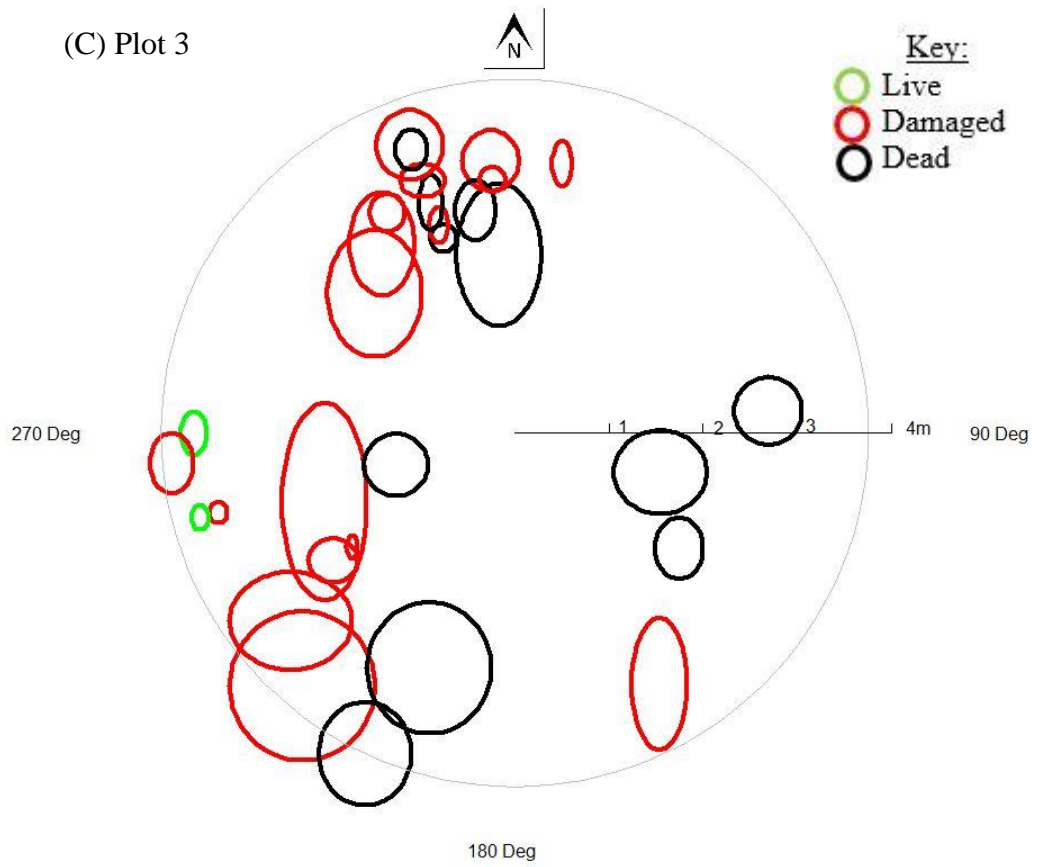


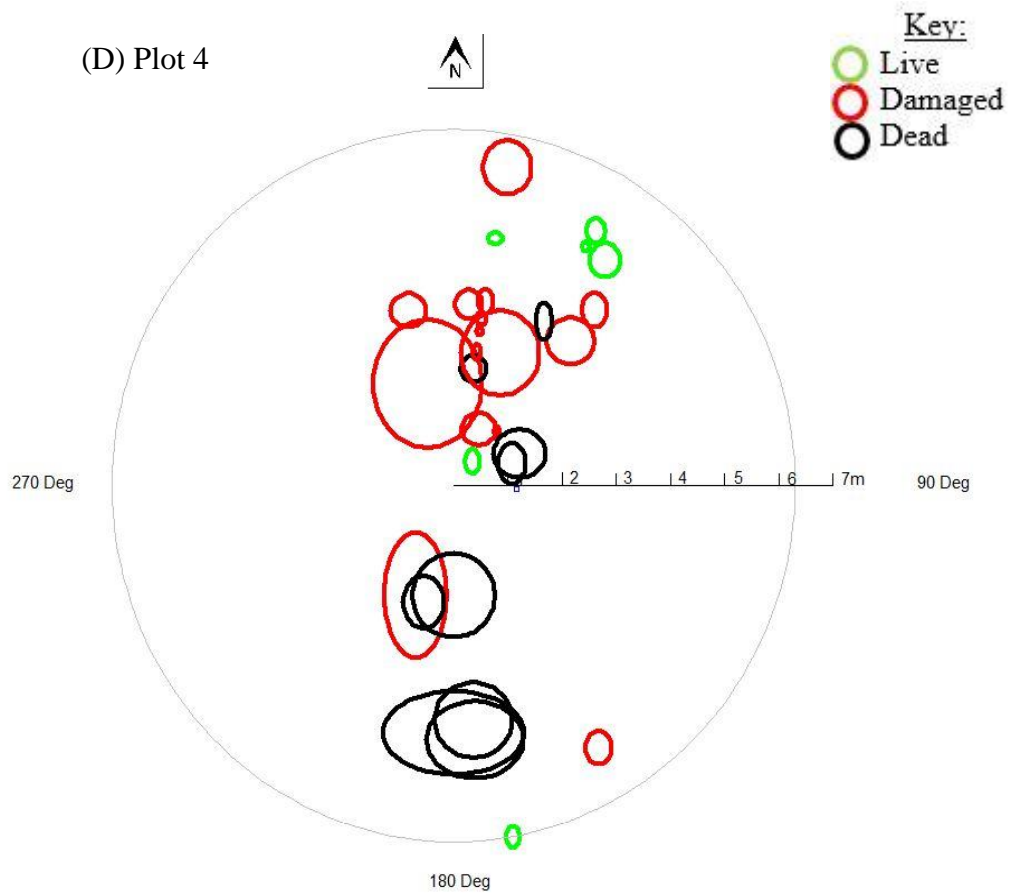
Fig A1.1 (A-V) Population structures showing the frequency of “Live”, “Damaged” and “Dead” *P. alpinus*, by height class, at each plot.



(C) Plot 3



(D) Plot 4



(E) Plot 5

Key:
Live
Damaged
Dead

7m 90 Deg

180 Deg

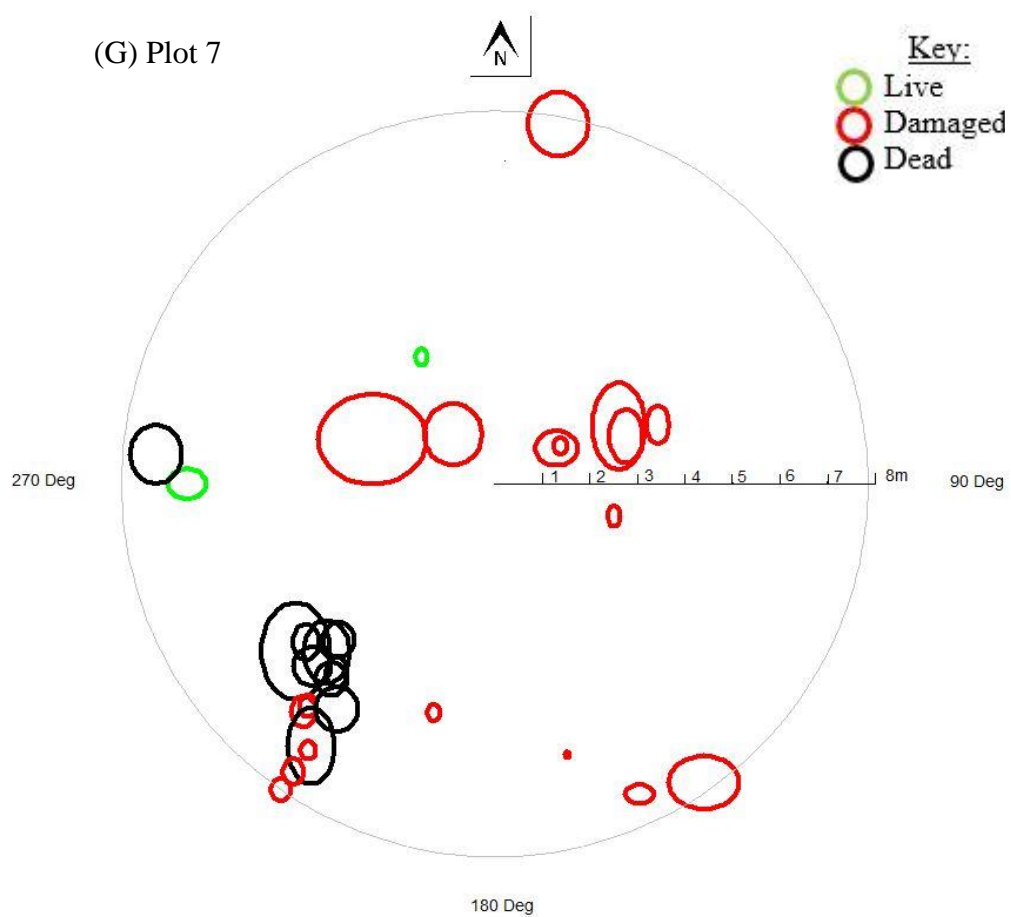
(F) Plot 6

Key:
Live
Damaged
Dead

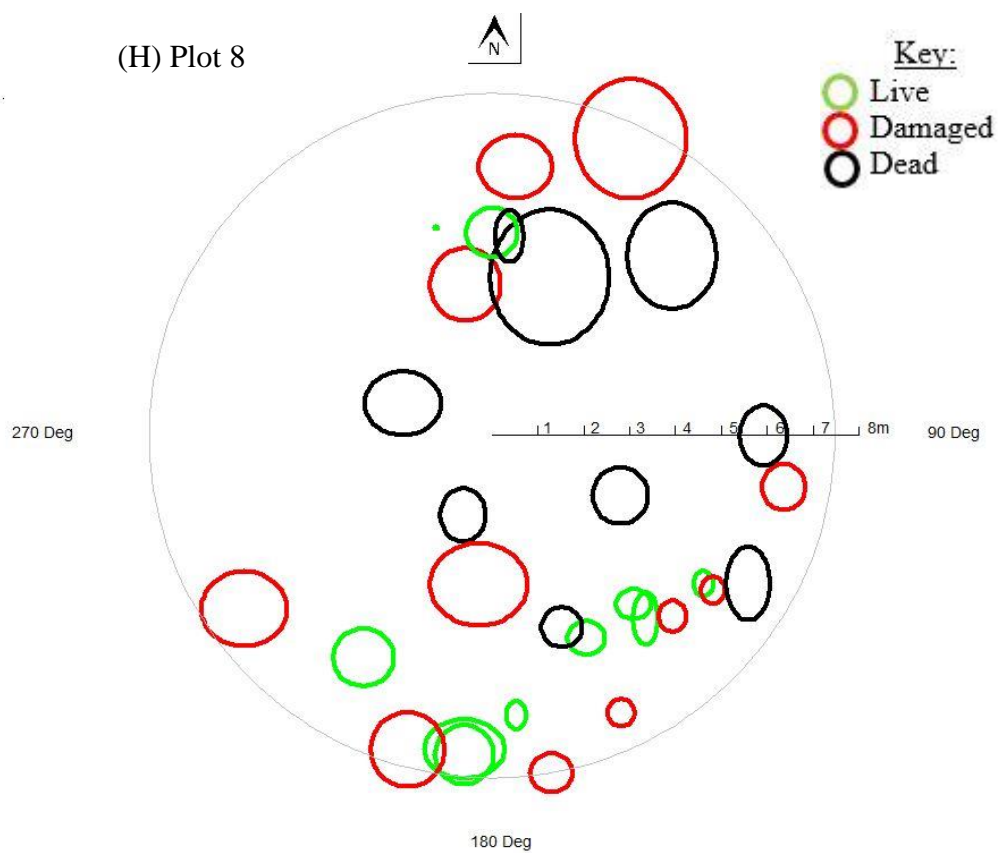
270 Deg 90 Deg 180 Deg

1 2 3 4 5 6 7m

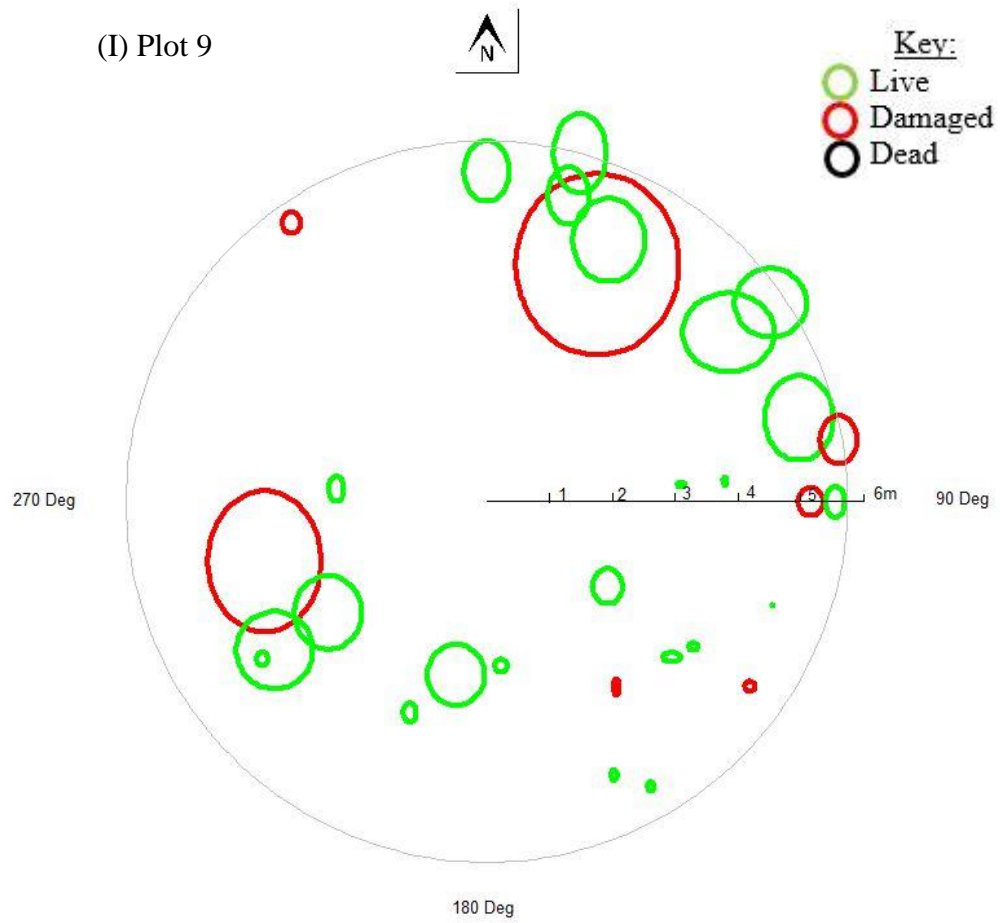
(G) Plot 7

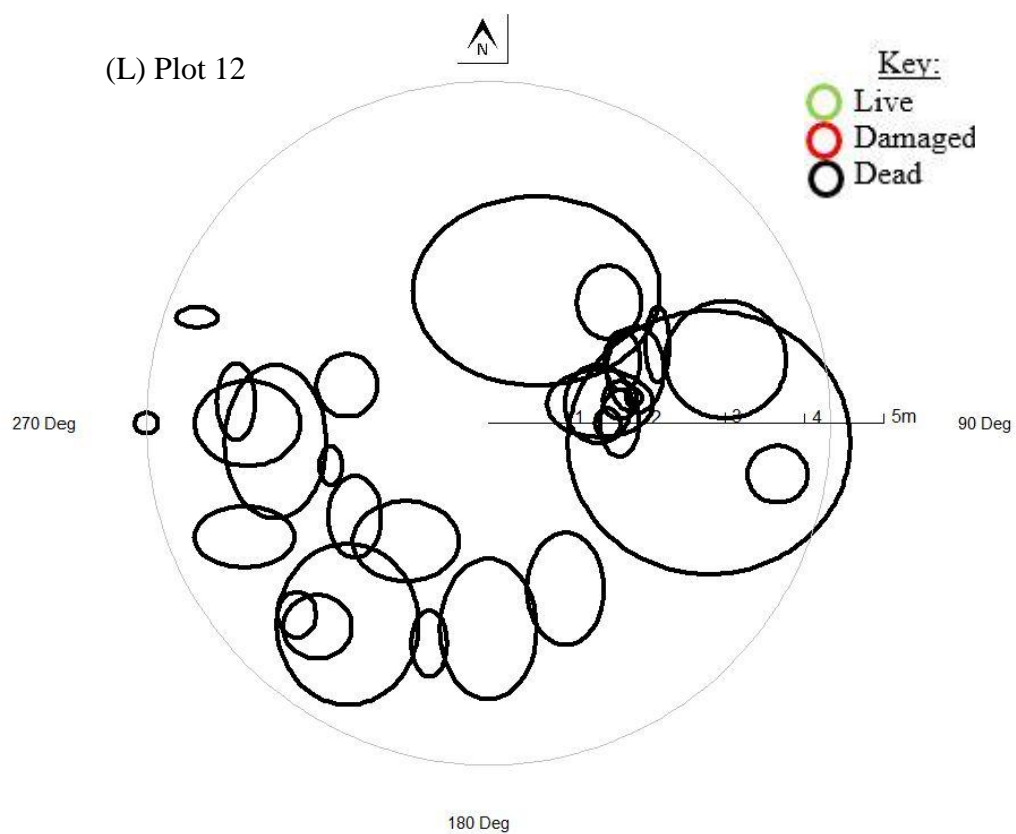
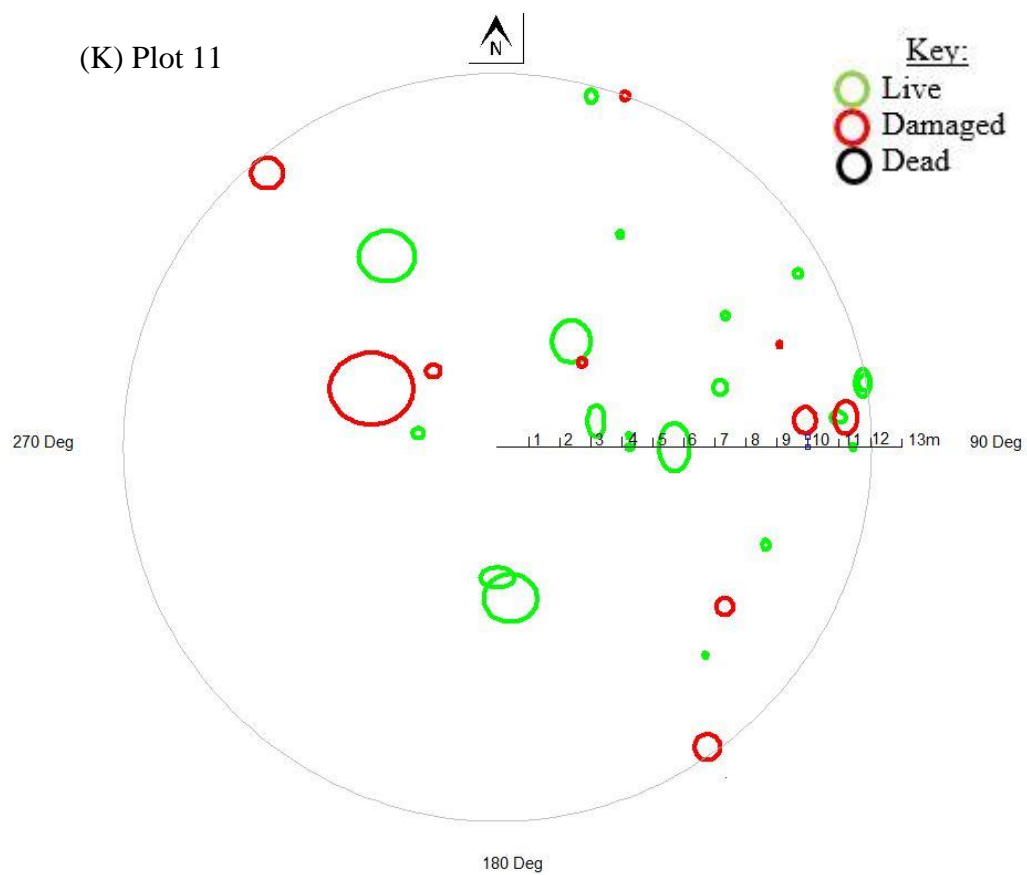


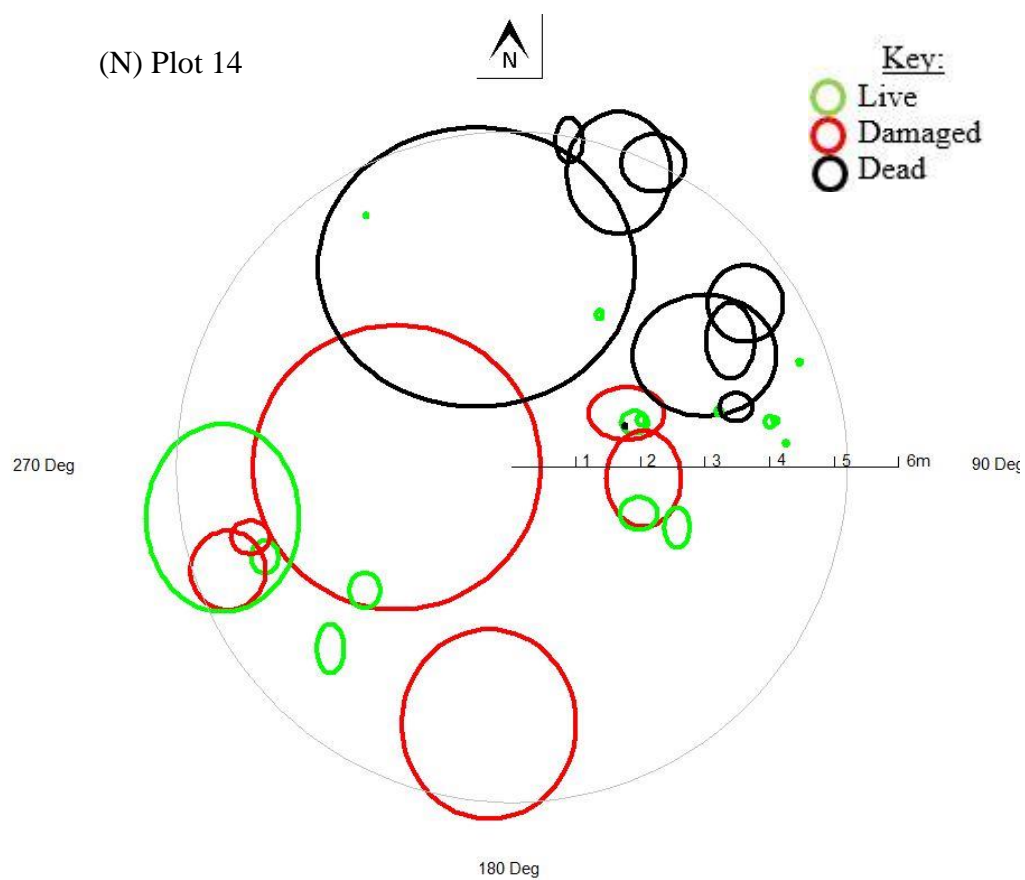
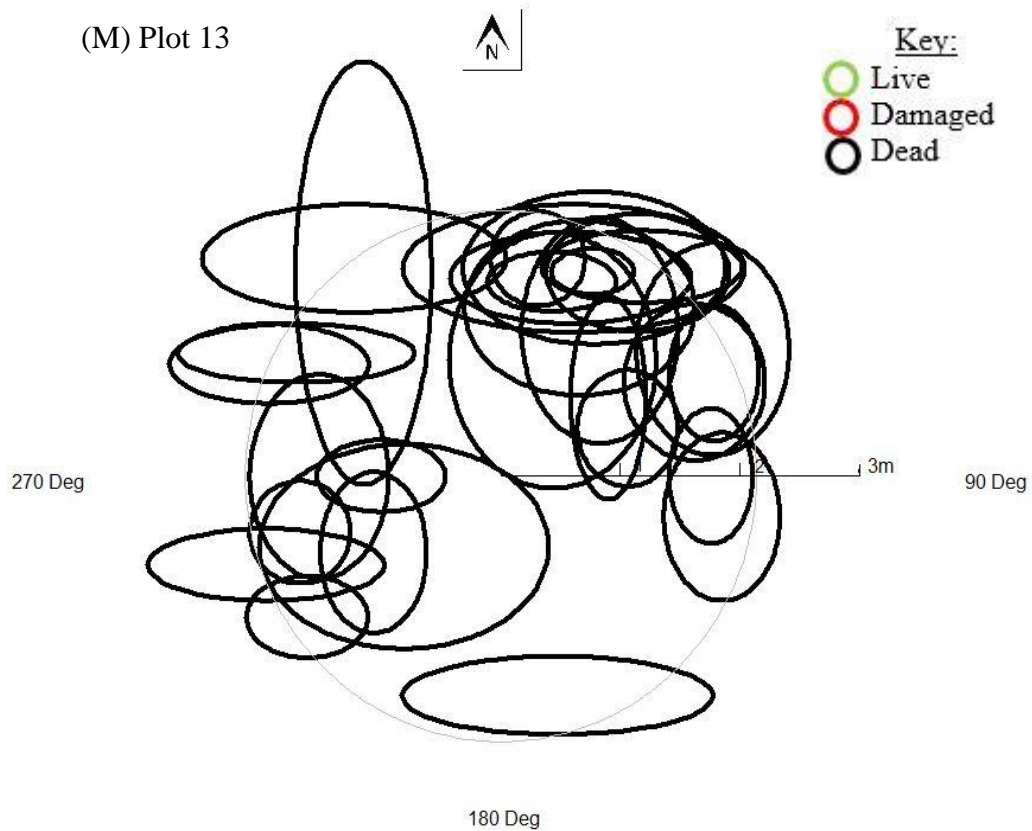
(H) Plot 8

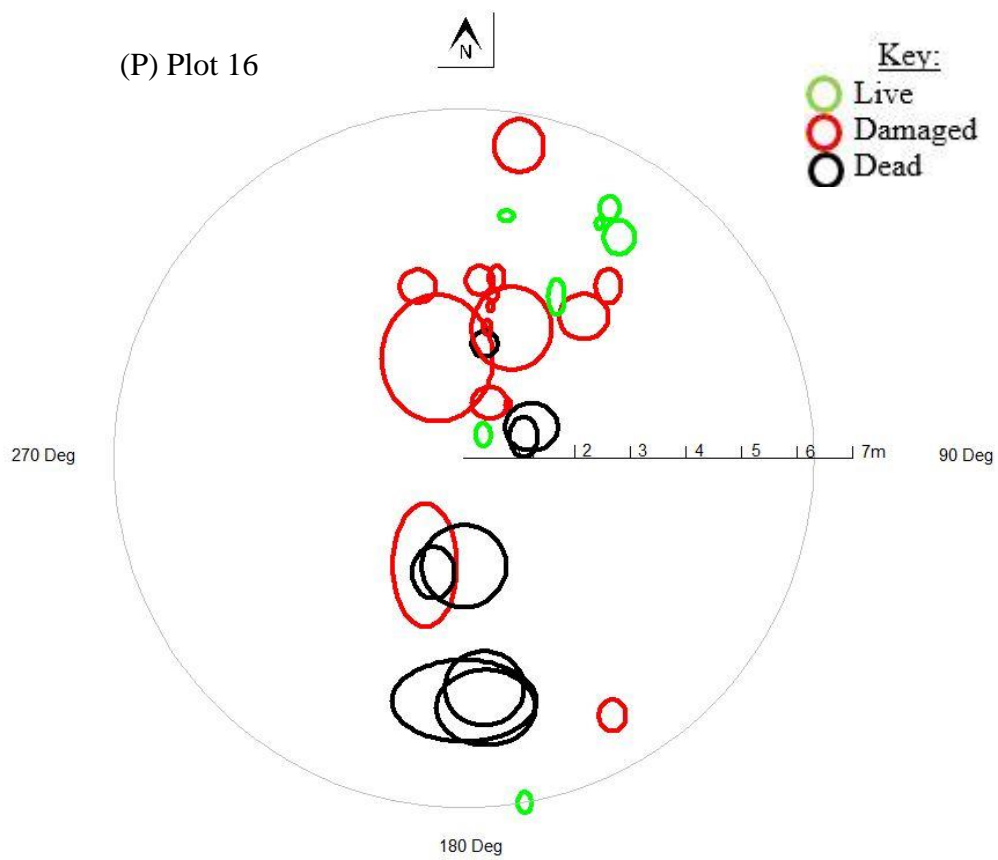
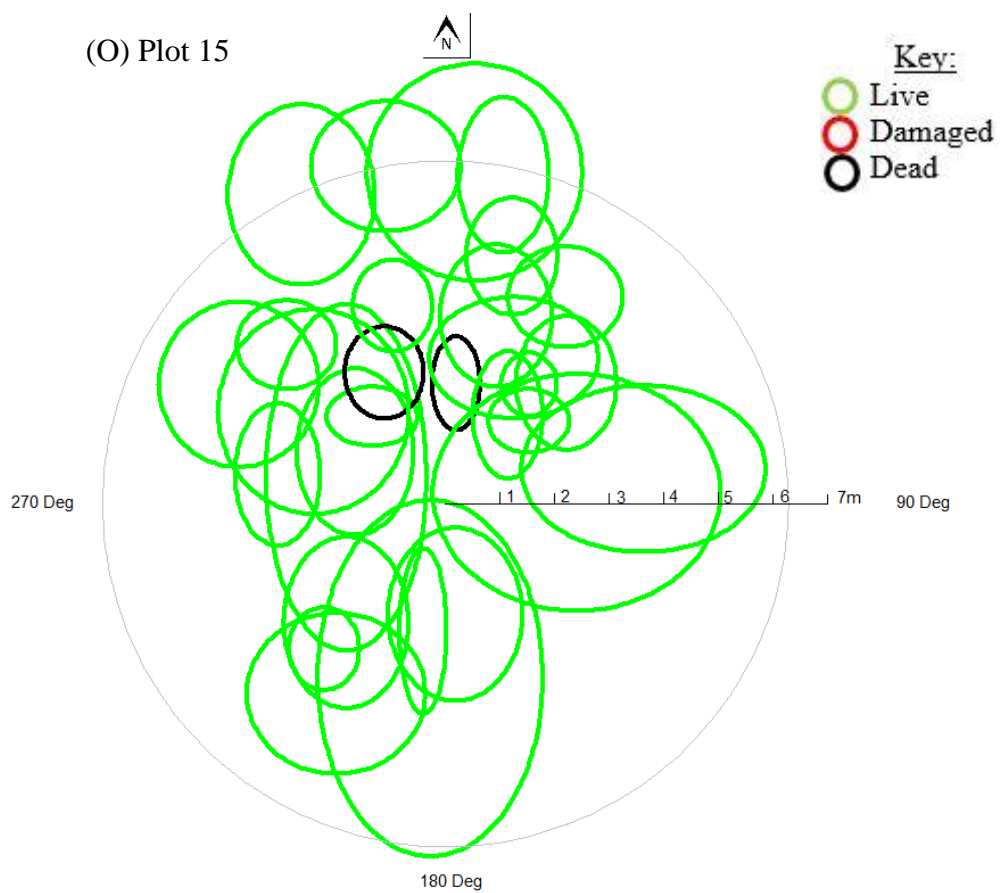


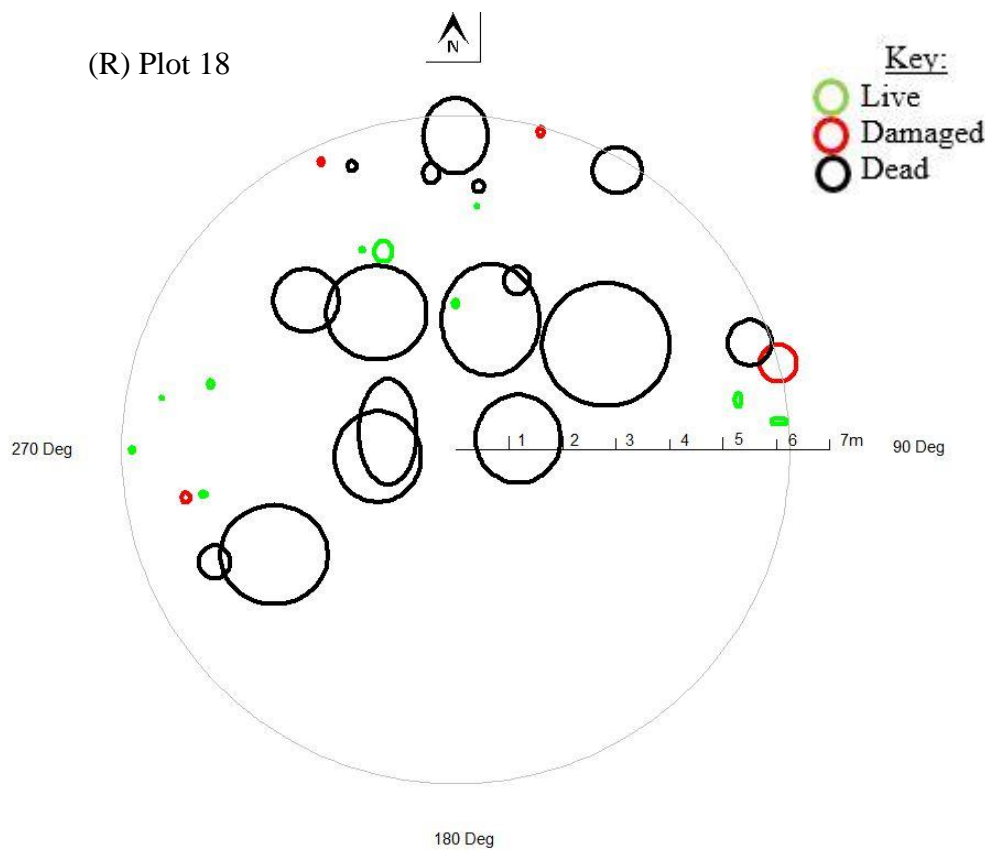
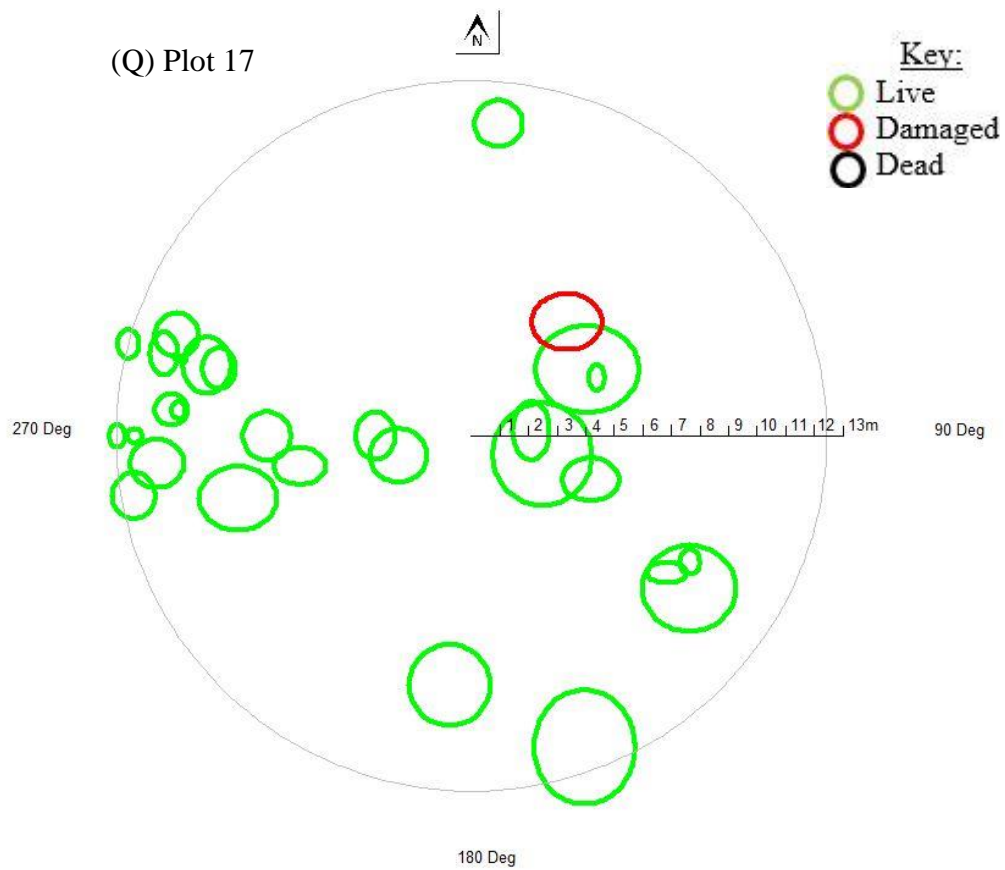
(I) Plot 9



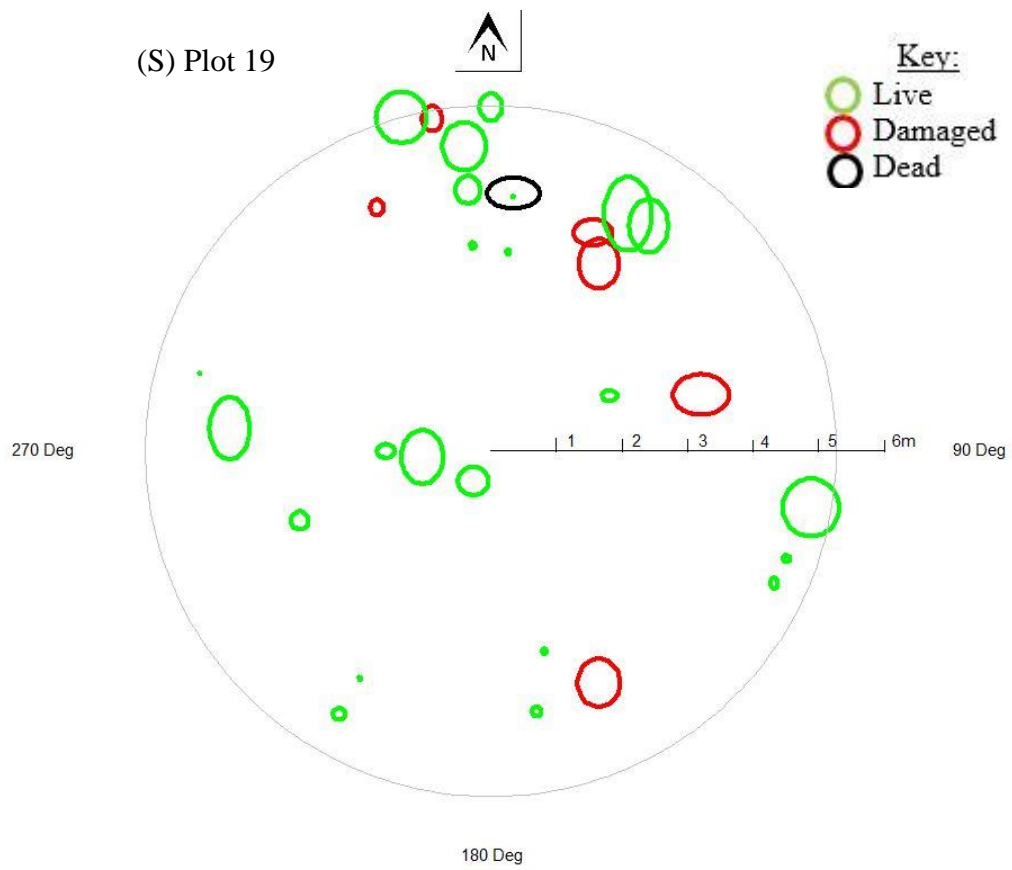




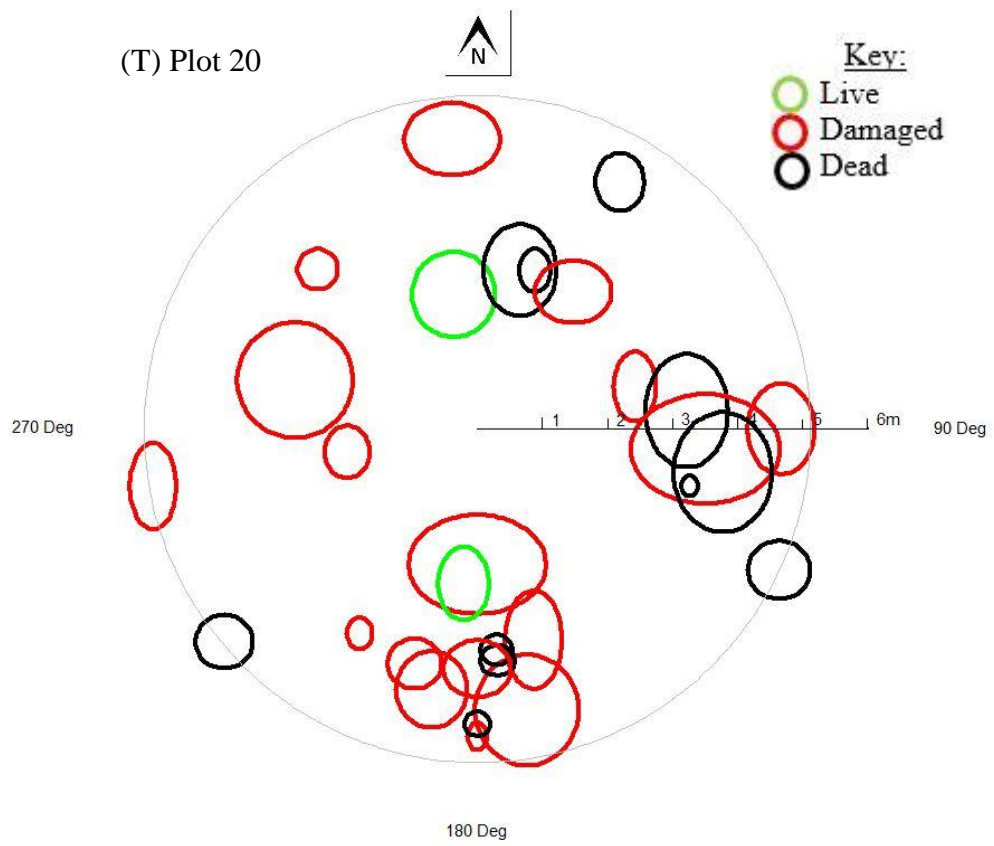




(S) Plot 19



(T) Plot 20



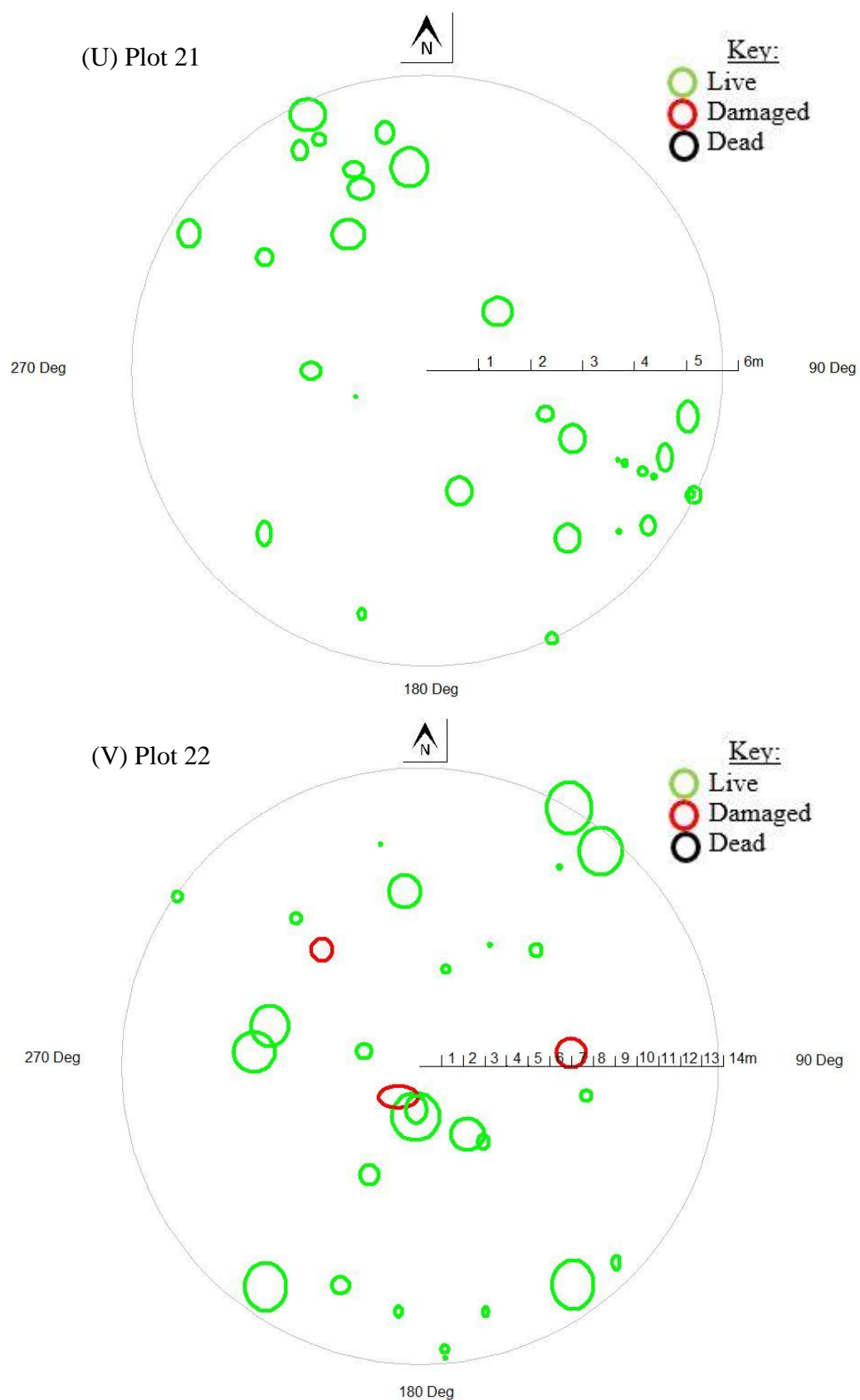


Fig A1.2 (A-V) Plot diagrams showing the distribution of “Live”, “Damaged” and “Dead” *P. alpinus* individuals within each plot.

Chapter 3

Species sensitivity to the 2012 Te Maari eruptions

3.1 Introduction

This chapter presents the results and discussion regarding species sensitivity to the 2012 Te Maari eruptions. The 10 most abundant vascular species are the focus of this research. Before presenting the research, relevant background information is provided.

3.1.1 Background Information

Plants in alpine environments have features that allow them to exist in stressful environments (Anthelme et al. 2014), however volcanic activity can both destroy or modify this vegetation. The impact of the volcanic activity depends on the type of activity and the characteristics of the vegetation (Dale 1989).

Ash fall is one type of activity which can affect plant growth, either by burial, overloading or affecting different physical or chemical process (De Schutter et al. 2015). Changes in soil probably have the most long term impacts on vegetation (Dale 1989), with ash affecting nutrient input, pH, and the capacity to exchange gas, water and heat with the atmosphere (Ayrís & Delmelle 2012). The depth of material deposited on the vegetation has a clear effect on survival, including deposition on top of snow cover (Dale 1989). Prolonged burial can reduce the size of shoots which can reduce survival in subsequent years (Zobel & Antos 1986). Ash three centimetres thick was recognised as the threshold for causing decay and subsequent recovery of vegetation cover, with shrubs and herbaceous vegetation more susceptible to damage from ash than trees (De Schutter et al. 2015). Hairs on leaves and fruits can cause ash to remain on the surface, with smooth and waxy leaves less prone to holding particles (Cook et al. 1981). This deposition may result in early abscission of fruits and leaves and well as structural failure and collapse of branches due to overloading (Ayrís & Delmelle 2012). It may also slow photosynthesis by blocking light or stomata, and change leaf water potentials (Cook et al. 1981). The size and position of the perennating organs can be a predictor of survival from volcanic activity, for example, trees can survive mudflows when

smaller species do not as their buds are high and less disturbed by the mudflow. Species with buds below the surface may survive also survive heavy ash deposits (Dale 1989). The life history of plants may also increase survival with some plants deferring growth until conditions become favourable, increasing their chance of survival (Dale 1989).

After the 1980 Mt. St. Helens eruption, geophytes (plants with subterranean dormant buds) and those who could regenerate from fragments, had the highest rates of survival (Adams et al. 1987), while acaulescent and prostrate species displayed damaged to vegetative parts due to the mechanical overloading of ash (Mack 1981). Species of small stature were also found to be the most affected species after the 1996 eruption of Mt. Ruapehu (Clarkson et al. 1997).

Pyroclastic density currents are another type volcanic activity that can cause death. The force of the PDC can remove trees from the substrate and the speed of particles suspended in the currents can cause abrasions. The high temperatures can disturb the hydrated tissues causing death, or charring (Blong 2013). Taller species will be more severely affected by PDCs (del Moral & Grishin 1999).

These differences in features and life histories will result is some species being more sensitive to particular types of volcanic disturbance, and therefore will have different rates of survival or recovery.

The tussock-shrublands northwest of Te Maari on Mt. Tongariro, were exposed to a PDC and a small ash fall during 2012. The westward PDC produced on the 6th of August 2012, was estimated to have initially travelled between 55 - 115 m/s (Lube et al. 2014), for approximately 60 seconds in duration, with estimated temperatures near the vent >64 °C and >51 °C at the distal end (Efford et al. 2014). An eruption followed on the 21st of November 2012, however this was less intense and only released a small amount of ash (Scott & Potter 2014) over this area. As events occurred in winter and spring, it is possible the landscape was covered in snow, however this could not be confirmed, and therefore the direct impact of the ash fall and heat on the surrounding species is unknown.

Examination of the subalpine vegetation in the months following the August

eruptions, showed there were “obvious differences in species susceptibility to the PDCs. For example, at the distal ends of the PDCs it was possible to find a completely browned apparently dead *Phyllocladus alpinus* tree alongside green and apparently unaffected *Podocarpus nivalis* sub-shrubs, while in the mid portions of the PDC, both of these species exhibited complete foliar browning” (Efford et al. 2014).

Knowing which species were the most affected by the PDC and therefore are the most sensitive, will help the monitoring of these species over time and provide an understanding of how continual volcanic disturbance affects secondary succession in a tussock-shrubland community. This data may also provide valuable information as to which plant species could be used as possible bio-indicators in the future, as well as provide quantitative data upon which to base management decisions.

These objectives are addressed by considering the following research question:

1. Was *P. alpinus* the species most affected by the volcanic disturbance?

3.2 Method

A point intercept method was used to yield proportions representative of the species in the canopy layer, which had maximum exposure to the PDC. The point intercept data was collected from the same 22 circular plots where the *Phyllocladus alpinus* data was measured (see Figure 2.5, Chapter 2. For overview of the entire study area see Figure 1.2, Chapter 1). This includes the same 4 x 30 m measuring tapes, radiating from the same central point. The four tapes were evenly spaced bearing approximately north, south, east and west, over top of the vegetation (see Figure 2.6, Chapter 2). Measurements were collected every 10 cm from the central stake to the longest distance recorded for the corresponding *P. alpinus*. For example, if the maximum distance for a *P. alpinus* in that plot was 4.60 m from the centre stake, the point intercept data was also measured along the tapes to 4.60 m. If however, the distance for the corresponding *P. alpinus* data set was 6.26 m, the point intercept data was recorded to 6.20 m; as no points were collected outside the *P. alpinus*

plots. Measurements were conducted using a 1 m high rod with a pointed tip, and standing as close to directly over top of the tape as possible. The first species (vascular and non-vascular) to make contact with the rod was recorded, including foliage blown onto the rod by the wind. If the foliage on the individual was living, the species was recorded as “alive”. If there was no foliage (for example a bare branch) or the foliage appeared to be dead, the species was recorded as “dead” (Figure 2.11). If no species were present at a point, the substrate was recorded.

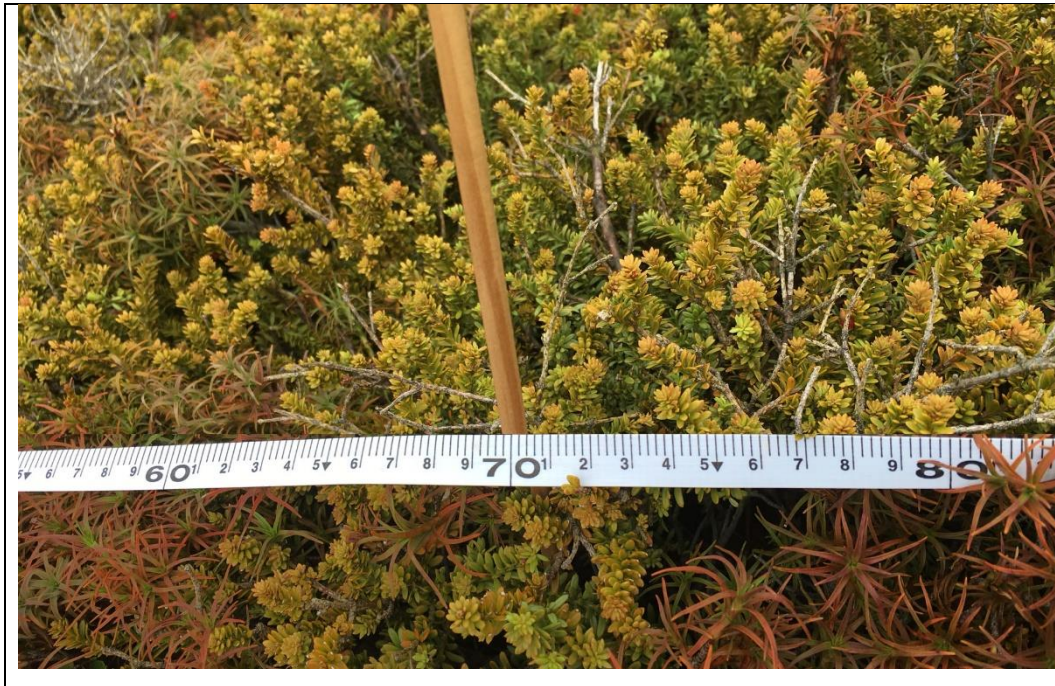


Figure 3.1 Example of equipment and method used to collect point intercept data. In this photograph *Podocarpus nivalis* is the first species to make contact with the rod and is therefore recorded as alive *P. nivalis*.

3.3 Results

The point intercept data revealed species differed widely in their proportions of foliage survival on Mt. Tongariro (Figure 2.16). Only 57.73% of points recorded found alive *Phyllocladus alpinus*, while 100% of *Gautheria colensoi* and *Coprosma cheesemanii* foliage was alive.

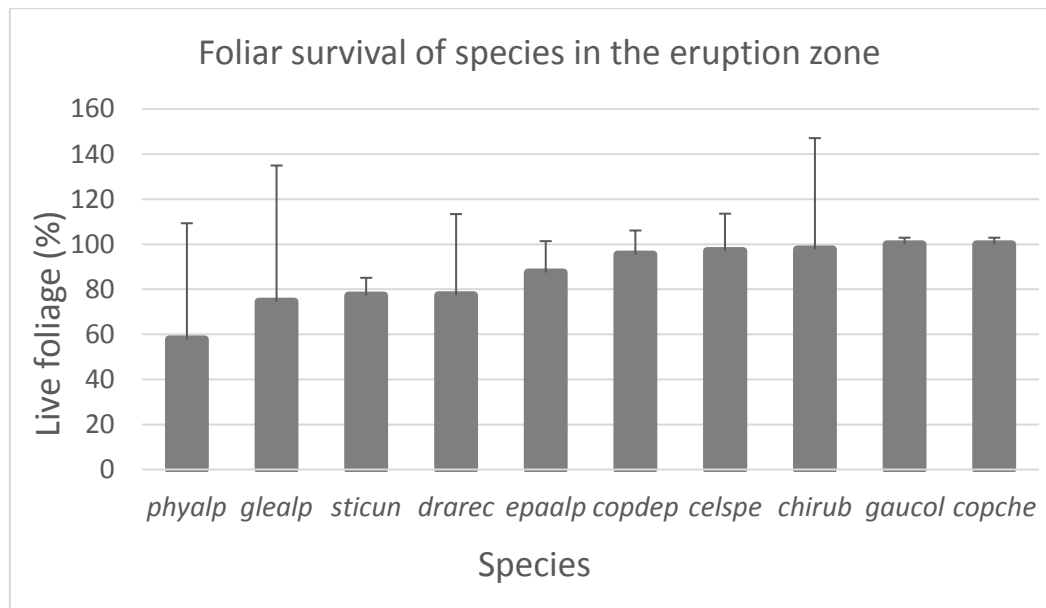


Figure 3.2 Foliar survival of the 10 most abundant species. Sample sizes were: phyalp n = 1055, glealp n= 271, sticun n=171, drarec n=1284, epaalp n=239, copdep n=218, celspe n =438, chirub n=1223, gaucol n=93, copche n=91.

3.4 Discussion

The point intercept data from the present study shows there is variation in species foliar survival, including those species whose foliage was browned by the PDCs during the 6th of August eruptions (Figure 2.12). As foliar survival was not quantified between the eruptions on the 6th of August and the 21st of November, damage specifically caused by the PDCs cannot be distinguished from that of the ash fall and PDCs combined. It should also be stated that the eruption on the 6th of August (winter) occurred close to midnight (Efford et al. 2014), when the ambient temperature would have been relatively low. The foliar damage caused from a sudden change in temperature (>64 °C and >51 °C) cannot be distinguished from foliar damage caused by the specific temperature.

Phyllocladus alpinus had the lowest foliage survival rate of 57.73% from the 10 most abundant species (Figure 2.1, chapter 2). This is expected as taller species receive maximum exposure to the PDCs force and heat, while also being the first species to collect particles from ash fall. Species of lower stature may be sheltered by taller species, and therefore PDCs affect taller species more severely (del Moral & Grishin 1999). Another aspect to consider are the morphological features. The phylloclades of *P. alpinus* are flat and therefore prone to ash and particle retention, however heat from the PDC was shown to brown phylloclades (Efford et al. 2014),

therefore the ash fall in November is unlikely to have affected foliar survival. The heat from the PDC may have affected the buds of *P. alpinus*, lowering the probability of resprout following the PDC. Dormant and adventitious buds of *P. alpinus* are highly resinous. They have not been seen to recover after individuals have been exposed to fire (Wardle 1969). As the heat from a PDC can resemble a fire, the temperature change of this resin within the bud may have caused damage and therefore result in a low foliar survival.

Other tall species in this area (which were less abundant than the top 10 species) include *Ozothamnus vauvilliersii*, and *Veronica odora* (shrubs). These species had even lower foliar survival of 27.6% (n=47) and 60.0% (n=71) respectively, however as their sample sizes were very small, this result must therefore be viewed with caution.

Although *P. alpinus* and other taller species were found to have low foliar survival, *Gleichenia alpina* and *Sticherus cunninghamii* (low growing ferns) were the second and third most affected species (within the 10 most abundant species) with 74.54% and 77.19% live foliage respectively (Figure 3.3). *Gaultheria colensoi* and *Coprosma cheesemanii*, also low growing species, always had live foliage, suggesting height is not the only factor determining foliar survival. These findings also suggest earlier assumptions of this research (Section 2.5.2, Chapter 2), that the PDC may not have always touched the ground and resulted in a higher rate of survival for lower plants, may not be correct.

The growth forms of these species vary, and may contribute to their respective foliar survivals. *G. alpina* (commonly known as alpine tangle fern), intertwines or tangles its repeatedly dividing stems with other plants or itself. This creates a mat like growth, which is difficult for objects to pass through, including particles suspended in the PDCs, which are moving at high speeds. *Gleichenia alpina* also has scales on its fronds (New Zealand Plant Conservation Network 2017h), which may catch these high speed particles in the PDC causing severe abrasions and/or retain ash particles which could cause salt damage and minimise photosynthesis. This damage maybe beyond a point of recovery, reflecting a low foliar survival for *G. alpina*.



Figure 3.3 *Gleichenia alpina* (background) and *Sticherus cunninghamii* (foreground). Image sourced from https://farm4.static.flickr.com/3268/2353871189_9254c8513e.jpg

Sticherus cunninghamii (also known as umbrella fern), has very delicate, soft new growth which would be very susceptible to desiccation and heat damage from PDCs. The adult form possess long, stiff, scaly rachises 12 – 30 cm in length; which droop in the form of an umbrella. The stipes are thin, long (20 – 50 cm), scaly and hairy (New Zealand Plant Conservation Network 2017i). The long, stiff, scaly fronds may therefore collect the fast moving particles in the PDC, increasing the force on the stipe, which being thin, may break. The scales on the fronds may also collect the particles moving in the PDC, damaging the fronds through abrasions. They may also increasing the retention of ash particles that could cause salt damage and therefore reflect the low foliar survival of *S. cunninghamii*.

The high foliar survival of *G. colensoi* in the present study (100% live) was initially surprising, as after the 1996 eruption on Mt. Ruapehu (also in the TNP), the foliar survival of *G. colensoi* was 40 – 60%. The primary volcanic event for that eruption however was ash, which accumulated in the horizontally-orientated leaves (Clarkson et al. 1997). In the present study, ash fall was minimal, with the PDCs the primary volcanic event. *Gaultheria colensoi* is probably better suited to withstand damage from PDCs as it has small coriaceous leaves 5 - 9 cm wide (New

Zealand Plant Conservation Network 2017g), which are less likely to be prone to desiccation (Figures 3.4 and 3.6).



Figure 3.4 Photograph showing the small coriaceous leaves *Gaultheria colensoi*

Coprosma cheesemanii, like *G. colensoi*, also has small leaves (Figure 3.5). They are glossy (New Zealand Plant Conservation Network 2017c) and spaced out along thick woody branches, that are low to the ground, and therefore provide stability and little resistance to PDCs particles, minimising damage and reflecting the high foliar survival.



Figure 3.5 Low growing, small leaved *Coprosma cheesemanii*.

Coprosma depressa is very similar to *C. cheesemanii*, in that it is low growing (even more so), possess small leaves, which are glossy and therefore probably well suited to withstand desiccation from PDC temperatures. One difference between *C. depressa* and *C. cheesemanii* is that *C. depressa* has stiff curled leaves (New Zealand Plant Conservation Network 2017d), which may slightly increase resistance to PDC currents and account for the slightly lower foliar survival compared to *C. cheesemanii*. Interestingly, *Dracophyllum recurvum* also possess stiff leaves and has a much lower foliar survival than the closely related *Dracophyllum longifolium* which has erect, needle like leaves (77.34 % and 96% respectively). This suggests wider, recurved leaves are detrimental to withstand PDCs. *Dracophyllum recurvum* leaves are also rough on the upper surface and are in a rosette formation, this may retain ash or PDC particles which could cause damage and minimise photosynthesis (Figures 3.6 and 3.7). *Dracophyllum* is prostrate (New Zealand Plant Conservation Network 2017e), which like *G. alpina*, makes it difficult for PDCs to penetrate and therefore provides resistance to the PDCs increasing abrasions and damage. Although *D. recurvum* is usually a hardy species, these morphological features combined may account for the relatively low foliar survival.

Epacris alpina is a bushy woody shrub with small, hard leaves 3 – 5 cm long (Figures 3.6 and 3.7) (New Zealand Plant Conservation Network 2017e). Although it has small hard leaves, which would be advantageous against the heat of the PDC to prevent desiccation, its bushy shrub growth form and hairs on the twigs would, like *G. alpina*, make it difficult for objects to pass through, including particles suspended in the PDCs, which are moving at high speeds. This would therefore increase abrasions and retain particles on the surface of the twigs, resulting salt damage.



Figure 3.6 Photograph showing (a) *Epacris alpina* (b) *Dracophyllum recurvum* (c) *Gaultheria colensoi*.

Celmisia spectabilis and *Chionochloa rubra* possess very different growth forms and yet they both had 97% foliage survival (Figure 3.7). *C. spectabilis* is a herb which is lowing growing in mats or cushions. It has soft leaves (30 – 180 mm long and 3 - 30 mm wide) which are coriaceous (New Zealand Plant Conservation Network 2017a) and therefore would provide little resistance to PDC particles and minimise desiccation from PDCs. Leaves do tend to be slightly recurved so ash may

collect in the leaf base, however as ash fall was minimal it does not appear to have affected foliar survival. *C. rubra* on the other hand is tall and possess rather “stiff”, slender, leaves compared with other grass species’. Although these stiff leaves are smooth and rush-like and approx. 1 m in length (New Zealand Plant Conservation Network 2017b), they are adapted to flex and rebound to the high winds that are associated with alpine environments. This feature could therefore allow *C. rubra* to move with force of the PDC without breaking.



Figure 3.7 Photograph showing (a) *Chionochloa rubra* (b) *Celmisia spectabilis* (c) *Dracophyllum recurvum* (d) *Epacris alpina*.

These results partially support Clarkson et al. (1997) and Mack (1981) in that growth form appears to affect the survival of species after volcanic disturbance, however contrary to Clarkson et al. (1997) and Mack (1981) the present study suggests taller species may be more affected. This is most likely due to PDCs being the primary volcanic disturbance, rather than ash fall. As height is only a component of foliar survival the present research only partially supports del Moral and Grishin (1999) who state taller species will most likely be more severely affected by PDCs. The low foliar survival of *Gleichenia alpina* and *Sticherus cunninghamii* who possess hairs and scales supports findings by Cook et al. (1981).

3.5 Summary and Recommendations

Foliar survival varies within the area affected by the PDCs, with *Phyllocladus alpinus* exhibiting the lowest foliar survival and is therefore the most sensitive species to the PDC. Species sensitivity appears to be based on height and morphological features. *Phyllocladus alpinus* and taller species showed less foliar survival, while small coriaceous or glossy leaves; or narrow flexible leaves appear advantageous morphological features. Species with stiff curved leaves had lower foliar survival compared to other species of the same genus, suggesting this growth form is detrimental. Hairs, scales and a dense growth form also appear to be a disadvantage for foliar survival from PDCs.

Although the point intercept method was time efficient and yielded proportions representative of the species in the canopy layer, it also resulted in less dominant species or species of a small stature having small sample sizes. My recommendation for further data collection on species sensitivity would be to measure more points within each plot and gain larger sample sizes. This would ensure there is sufficient data on species such as *Ozothamnus vauvilliersii*, and *Veronica odora* (shrubs) to allow for a thorough investigation of the foliar survival between shrubs and other growth forms/heights.

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Appendices

APPENDIX TWO

Table A2.1 List of all species included in species sensitivity data set.

Code	Species name	Family	Common names
andemp	<i>Androstoma empetrifolium</i>	Ericaceae	Bog mingimingi
aniaro	<i>Anisotome aromatica</i>	Umbelliferae	Aromatic aniseed, Kopoti, Mountain carrot
astfra	<i>Astelia fragrans</i>	Asteliaceae	Bush flax, Kakaha
blemon	<i>Blechnum montanum</i>	Blechnaceae	Mountain kiokio
blepen	<i>Blechnum penna-marina</i>	Blechnaceae	Alpine hard fern
brabid	<i>Brachyglottis bidwillii</i>	Compositae	
brysp.	<i>Bryum</i> sp.		
calvul	<i>Calluna vulgaris</i>	Ericaceae	Heather
camp.	<i>Campylopus</i> sp.		
carsp.	<i>Carex</i> sp.		
celspe	<i>Celmisia spectabilis</i> subsp. <i>spectabilis</i>	Compositae	Mountain daisy
chirub	<i>Chionochloa rubra</i> subsp. <i>rubra</i> var. <i>rubra</i>	Gramineae	Red tussock
copche	<i>Coprosma cheesemanii</i>	Rubiaceae	
copdep	<i>Coprosma depressa</i>	Rubiaceae	
copdmo	<i>Coprosma dumosa</i>	Rubiaceae	
copfoe	<i>Coprosma foetidissima</i>	Rubiaceae	Stinkwood
copper	<i>Coprosma perpusilla</i>	Rubiaceae	
coppse	<i>Coprosma pseudocuneata</i>	Rubiaceae	
deyave	<i>Deyeuxia avenoides</i>	Gramineae	Mountain oat grass
dralon	<i>Dracophyllum longifolium</i> var. <i>longifolium</i>	Ericaceae	inanga, inaka
drarec	<i>Dracophyllum recurvum</i>	Ericaceae	Mountain inaka
drasub	<i>Dracophyllum subulatum</i>	Ericaceae	Monoao
epaalp	<i>Epacris alpina</i>	Ericaceae	
gahpro	<i>Gahnia procera</i>	Cyperaceae	Giant sedge, Mountain Gahnia
gaucol	<i>Gaultheria colensoi</i>	Ericaceae	Snowberry
gaudep	<i>Gaultheria depressa</i>	Ericaceae	Snowberry
gaumac	<i>Gaultheria macrostigma</i>	Ericaceae	Prostrate snowberry
genbel	<i>Gentianella bellidifolia</i>	Gentianaceae	Gentian
glealp	<i>Gleichenia alpina</i>	Gleicheniaceae	Alpine tangle fern
grilit	<i>Griselinia littoralis</i>	Griselinaceae	Broadleaf
hiered	<i>Hierochloa redolens</i>	Gramineae	Holy grass, Karetu
hisinc	<i>Histiopteris incisa</i>	Dennstaedtiaceae	Water fern
hyprad	<i>Hypochaeris radicata</i>	Compositae	Cats ear
lepjsj	<i>Leptecophylla juniperina</i> subsp. <i>juniperina</i>	Ericaceae	Prickly mingimingi
leplax	<i>Lepidothamnus laxifolius</i>	Podocarpaceae	Pigmy pine
lepsc	<i>Leptospermum scoparium</i>	Myrtaceae	Manuka

lichen			
lycfas	<i>Lycopodium fastigiatum</i>	Lycopodiaceae	Alpine club moss
myrdiv	<i>Myrsine divaricata</i>	Primulaceae	Weeping matipo
myrnum	<i>Myrsine nummularia</i>	Primulaceae	Creeping matipo
orepec	<i>Oreobolus pectinatus</i>	Cyperaceae	
ozovau	<i>Ozothamnus vauvilliersii</i>	Compositae	Mountain tauhinu, Mountain cottonwood
paesca	<i>Paesia scaberula</i>	Dennstaedtiaceae	Ring fern, Scented fern
penpum	<i>Pentachondra pumila</i>	Ericaceae	
phyalp	<i>Phyllocladus alpinus</i>	Podocarpaceae	Mountain toatoa
poasp.	<i>Poa</i> sp.		
podlae	<i>Podocarpus laetus</i>	Podocarpaceae	Hall's Totara
podniv	<i>Podocarpus nivalis</i>	Podocarpaceae	Snow totara
psecol	<i>Pseudowintera colorata</i>	Winteraceae	Horopito
psecvc	<i>Pseudopanax colensoi</i> var. <i>colensoi</i>	Araliaceae	Mountain five finger, Orihou
raclan	<i>Racomitrium lanuginosum</i>	Grimmiaceae	
rausim	<i>Raukaua simplex</i>	Araliaceae	
rytgra	<i>Rytidosperma gracile</i>	Gramineae	Dainty bristle grass
rytset	<i>Rytidosperma setifolium</i>	Gramineae	Bristle tussock
senvul	<i>Senecio vulgaris</i>	Compositae	Groundsel
sticun	<i>Sticherus cunninghamii</i>	Gleicheniaceae	Umbrella fern
uncsp.	<i>Uncinia</i> sp.		
verodo	<i>Veronica odora</i>	Plantaginaceae	
vertet	<i>Veronica tetragona</i>	Plantaginaceae	Whipcord hebe
viofil	<i>Viola filicaulis</i>	Violaceae	Forest violet
wahpyg	<i>Wahlenbergia pygmaea</i>	Campanulaceae	Mountain harebell

Table A2.2 Matrix of data collected for each plot. “A” means alive, “D” means dead, “0” means in plot but not selected with point intercept equipment. Empty cell means species not located at that plot.

		Plot #																							
Species		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Total	% alive
drarec	A	27	14	32	34	61	69	85	79	43	13	96			1		131	73	12	44	47	24	108	993	77.34
	D	67	12	8	36	0	4	36	16	3	26	12			0		24	3	7	10	16	1	10	291	
chirub	A	45	51	23	17	14	34	28	58	58	96	83			16		148	50	167	41	24	73	169	1195	97.71
	D	0	0	0	0	0	0	1	0	1	0	7			0		3	16	0	0	0	0	0	28	
phyalp	A	0	0	12	23	36	26	0	0	7	0	21	0	0	6	237	40	78	2	18	36	3	64	609	57.73
	D	19	35	26	25	5	3	0	50	0	7	0	61	61	105	0	1	0	29	0	16	0	3	446	
celspe	A	39	16	20	18	33	16	46	21	7	6	22		0	0		41		2	34	13	33	58	425	97.03
	D	0	3	0	2	0	0	0	0	4	1	1		0	0		0		0	2	0	0	0	13	
glealp	A											52					15	135					0	202	74.54
	D											27					7	35					0	69	
epaalp	A	1	1	0	0	6	0	23	0	9	0	28					40	0		24	18	30	29	209	87.45
	D	0	0	0	0	0	0	0	0	0	0	0					20	0		4	2	2	2	30	
copdep	A	0	1	16	28	35	14	25	8	15	5	8	4	0	7		0	0	0	2	7	6	27	208	95.41
	D	0	0	0	0	0	3	5	0	0	1	0	0	0	0		0	0	0	0	0	0	1	10	
sticun	A	1	23	8	5	23	0	12		16	5	14	0		4		0	14	0		7			132	77.19
	D	0	4	1	0	3	0	7		9	0	7	4		0		0	4	0		0			39	
gaucol	A	8	2	2	7	2	5	8	11	3	3	7	3		1		3	2	3	2	9	5	7	93	100.00
	D	0	0	0	0	0	0	0	0	0	0	0	0		0		0	0	0	0	0	0	0	0	
copche	A	16			0				11		0						32	0		9		5	18	91	100.00
	D	0			0				0		0						0	0		0		0	0	0	
leplax	A	3	4		0	0		14	0	27	5	21					0		0	3		0	5	82	92.13
	D	3	0		0	0		1	0	3	0	0					0		0	0		0	0	7	

podniv	A	0	0	9		1	4	11	0	0	21	1		4		4		4	0	0	11	0	70	81.40	
	D	5	0	0		0	0	2	0	0	0	9		0		0		0	0	0	0	0	16		
verodo	A	0		0	4	10	20		0	1	0			8				0		0		0	43	60.56	
	D	0		0	0	6	4		3	0	0			15				0		0		0	28		
myrdiv	A		3	0	0	8	2	5	0		0	0		0	2	12	0	34		0	0		0	66	98.51
	D		0	0	0	0	0	0		0	0		0	1	0	0	0		0	0		0	1		
dralon	A	0		0					0			5					28	15					0	48	96.00
	D	0		0					0			0					2	0					0	2	
ozovau	A				0					0	0	2		11		0	0	0				0	13	27.66	
	D				1					0	0	28		5		0	0	0				0	34		
lepsco	A											6					25	3			6	0	40	90.91	
	D											3					0	1			0	0	4		
lichen	A				0				0	0						0			0		11	19	30	81.08	
	D				0				0	0						7			0		0	0	7		
coppse	A	1		0	0	0	8	0	0	0	5	0	0	0	9	0	0	0		0			23	71.88	
	D	0		0	0	7	2	0	0	0	0	0	0	0	0	0	0	0		0			9		
penpum	A			0	0	0	0	0	0	0	0	1					7		0	1	3	2	5	19	86.36
	D			0	0	0	0	0	0	0	0	0					0		0	1	0	1	1	3	
gahpro	A				5	0	3			5	0			3										16	100.00
	D				0	0	0			0	0			0										0	
brabid	A						14			2												0	16	100.00	
	D						0			0												0	0		
copdmo	A	2												3	0	0	6	2						13	100.00
	D	0												0	0	0	0	0						0	
rytgra	A	0	2			0				1								0	1	0	6		10	100.00	
	D	0	0			0				0								0	0	0	0		0		

grilit	<i>A</i>	0		0	0	6	0		0	0	3		0	0		0	0	9	100.00
	<i>D</i>	0		0	0	0	0		0	0	0		0	0		0	0	0	
rytset	<i>A</i>		0			0	0			2	0		0	0		2	0	4	100.00
	<i>D</i>		0			0	0			0	0		0	0		0	0	0	
hiered	<i>A</i>			0	0	0	0	0			2			0	1	1	0	0	100.00
	<i>D</i>			0	0	0	0	0			0			0	0	0	0	0	
raclan	<i>A</i>													3			0	0	100.00
	<i>D</i>													0			0	0	
genbel	<i>A</i>		0						2	0	0			2			0	1	100.00
	<i>D</i>		0						0	0	0			0			0	0	
drasub	<i>A</i>				4													0	100.00
	<i>D</i>				0													0	
orepec	<i>A</i>																0	2	100.00
	<i>D</i>																0	0	
lepjsj	<i>A</i>												3						100.00
	<i>D</i>												0						
uncsp.	<i>A</i>	0	0		3		0		0				0	0			0		100.00
	<i>D</i>	0	0		0		0		0				0	0			0		
astfra	<i>A</i>					0	3		0			0	0	0	0				100.00
	<i>D</i>					0	0		0			0	0	0	0				
aniaro	<i>A</i>	1	0	0		0	0	0	0		0	0	0	0	1	0		0	100.00
	<i>D</i>	0	0	0		0	0	0	0		0	0	0	0	0	0		0	
deyave	<i>A</i>								0		0	2				0			100.00
	<i>D</i>								0		0	0				0			
myrnum	<i>A</i>				0		0	0	0	0	0					0	0	0	100.00
	<i>D</i>				0		0	0	0	0	0					0	0	0	

[illegible]

paesca	<i>A</i>	0	0	0	0	0				0	0.00
	<i>D</i>	0	0	0	0	0				0	
hisinc	<i>A</i>		0	0	0	0				0	0.00
	<i>D</i>		0	0	0	0				0	
senvul	<i>A</i>			0				0		0	0.00
	<i>D</i>			0				0		0	
copfoe	<i>A</i>				0		0			0	0.00
	<i>D</i>				0		0			0	
brysp.	<i>A</i>				0	0				0	0.00
	<i>D</i>				0	0				0	
carsp.	<i>A</i>				0					0	0.00
	<i>D</i>				0					0	
blemon	<i>A</i>				0					0	0.00
	<i>D</i>				0					0	
podlae	<i>A</i>					0			0	0	0.00
	<i>D</i>					0			0	0	
viofil	<i>A</i>					0				0	0.00
	<i>D</i>					0				0	
gaumac	<i>A</i>						0		0	0	0.00
	<i>D</i>						0		0	0	
hyprad	<i>A</i>						0			0	0.00
	<i>D</i>						0			0	

Chapter 4

Vegetation development of impact craters formed by the 2012 Te Maari eruptions

4.1 Introduction

This chapter describes the pattern and process of primary and secondary succession initiated by ballistic projectiles from the August 6, 2012 Te Maari eruptions. The bases of this study is the re-measurement of 15 craters, initially measured in March 2013, some 6 months after the eruption. Before presenting the research, relevant background information is provided. For an overview of the study area and detailed information of the eruptions, see section 1.3, Chapter 1.

4.1.1 Background information

Three directional explosions from Te Maari on the 6th of August 2012, produced an estimated 13,200 ballistic projectiles, predominately to the north, east, and west of Te Maari (Breard et al. 2014). These projectiles created impact craters on the surface of Mt. Tongariro, ranging in size, with more than 2200 larger than 2.5 m in diameter (Figure 4.1) (Breard et al. 2014; Fitzgerald et al. 2014).



Figure 4.1 Crater 4, an example of a crater created from a ballistic projectile during the 2012 eruption of Te Maari. Photograph courtesy of Jackson Efford.

The second and largest explosion, propelled projectiles westward towards the tussocklands, and created an area of high impact crater concentration, approximately 1000 – 1300 m west of Te Maari (Figure 4.2).

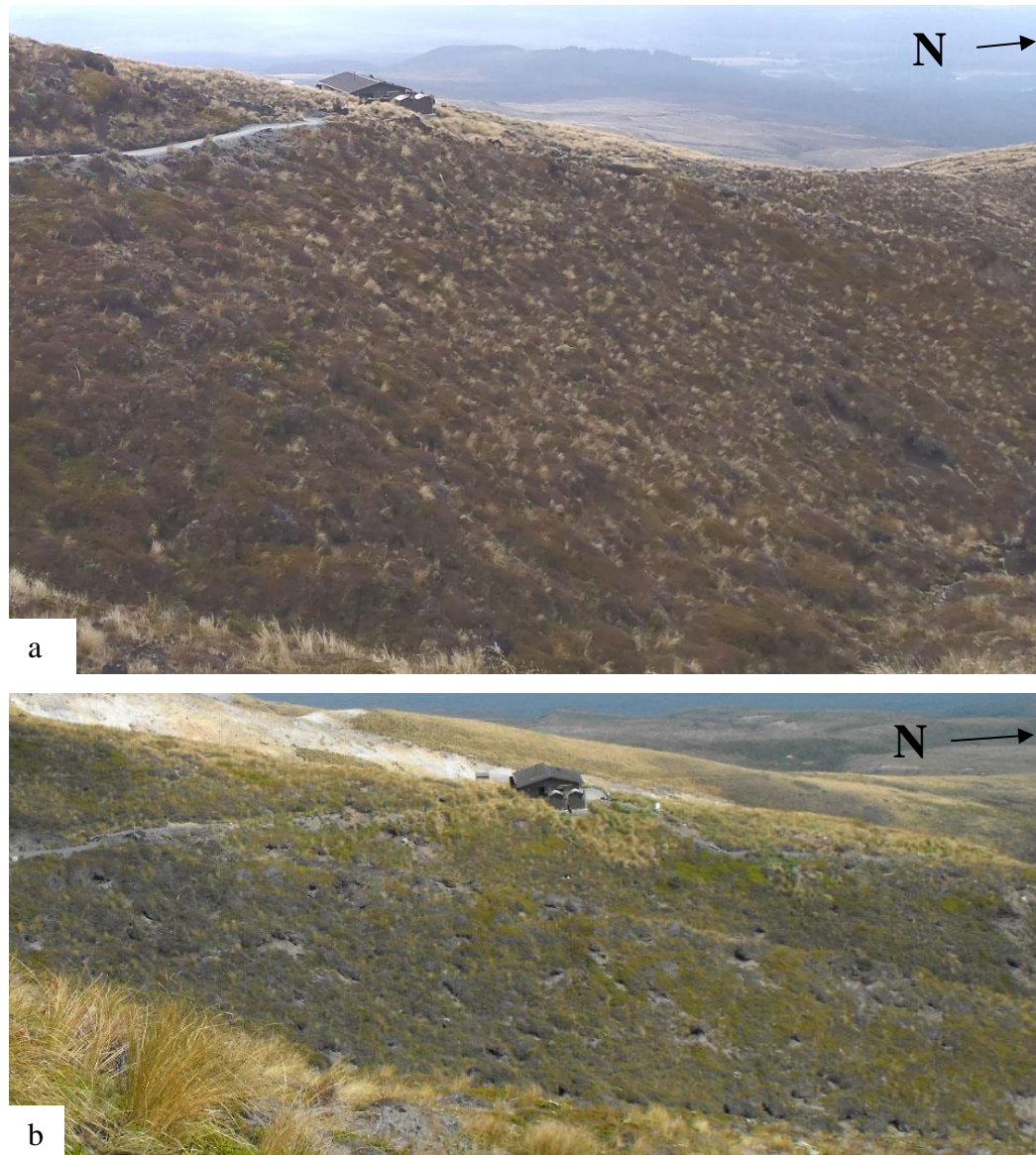


Figure 4.2 Photographs showing the landscape on Mt Tongariro near the Ketetahi Hut (a) before the eruption (b) after the eruption with the impact craters. Photographs were taken by Bruce Clarkson in (a) March 2012 (b) January 2013.

The projectiles were categorised into four lithologies: Type 1 = dense andesitic lava, Type 2 = andesitic scoria, Types 3 = breccia, agglomerates and agglutinate, and Type 4 = intermediate density andesitic lava (Breard et al. 2014; Fitzgerald et al. 2014). These different lithologies varied in density and though most projectiles were launched at an angle of less than 15 degrees to the horizontal (Breard et al. 2014), the various densities and sizes produced projectiles with an array of

velocities and kinetic energies. (Breard et al. 2014).

These variations in kinetic energy combined with the low growing vegetation and substrate “composed of non-compacted, soft pumice-rice, Taupo Pumice Ignimbrite, capped by a firmer brown weathered andesitic ash-sourced topsoil” (Breard et al. 2014); resulted in projectiles of 0.23 to 0.4 m in diameter causing crater diameters of 2.5 m and 3.5 m respectively (Breard et al. 2014). Some of the projectiles were preserved within these large craters while others were “shattered and scattered”, buried or were missing (Breard et al. 2014).

The low growing vegetation within the tussockland, dominated by *Chionochloa rubra* and *Dracophyllum recurvum* (Atkinson 1981), was often buried, either by the direct impact of the projectile or by the displacement of the substrate. The debris aprons that blanketed the surrounding vegetation were on average 110% greater in size than the craters diameter (Fitzgerald et al. 2014) and therefore a relatively small projectile could affect a large area of vegetation.

Pyroclastic density currents of approximately ≥ 64 °C (Efford et al. 2014) also blanketed vegetation in this area during the eruption (Lube et al. 2014) resulting in some species experiencing browning and loss of foliage (Efford et al. 2014). Ash produced during this eruption drifted eastward, away from this study area however a subsequent eruption on the 21st of November 2012 placed a thin layer of ash on the vegetation in this area, southwest of the vent (Pardo et al. 2014). More information regarding the PDC, ash fall and associated effects on vegetation in this area can be located in Section 3.1.1, Chapter 3.

There is no published ecological literature closely comparable to the research outlined here. The only studies on impact craters found described the effects of asteroids or comet impacts at a regional scale (Cockell & Lee 2002; Cockell et al. 2003), forming craters of a much larger scale than those presented in this study. An unpublished report found on impact craters formed by military shelling near Waiouru (Kingett-Mitchell Ltd 1999) provided an analogous comparison.

“From an ecological point of view impacts present an important addition to the overall picture of how ecosystems can be disturbed and how they can recover”

(Cockell et al. 2003), as both primary and secondary succession can be involved with a single impact crater.

The intra-crater space can be a habitat for primary succession as the impact of projectiles often involves extreme temperatures that can devoid the soil of all life. These extreme temperatures can also volatilize the macronutrients in the soil rendering it oligotrophic and difficult to recolonise (Cockell et al. 2003). On the other hand, the crater basin can create some shade, and protect colonising plants from wind. The depression in the crater can also trap water through rain or snow melt, resulting in significantly more vegetation cover in the crater than the surrounding area (Cockell & Lee 2002).

The vegetation directly outside the crater (the debris apron), gives rise to the opportunity for secondary succession. This is important as we know “successions, especially those with partial disturbance, are difficult to fit into successional models” (Clarkson 1990); however application of succession theory will be improved if biotic factors are better understood (del Moral & Grishin 1999). The examination of the species composition in these debris aprons over time can therefore increase understanding as to which mechanisms are driving change.

The aim of this study is to provide quantitative data to increase the understanding of which mechanism/s influence both primary succession and secondary succession following volcanic disturbance; which can contribute to the development of accurate models of succession.

The objective of this study is to examine the species composition of the craters and consider the question:

1. How has the species composition of the impact craters changed over time?

4.2 Method

Fifteen craters near the Ketetahi hut that were formed from ballistic projectiles ejected westward from Te Maari were examined in March 2013 (Figure 4.3. For overview of the entire study area see Figure 1.2, Chapter 1). The GPS co-ordinates of these craters were recorded as well as the maximum depth and two diameter measurements for each crater. The presence and percent cover of vascular plants was recorded for species inside the crater and within a 1 m perimeter outside of the crater rim. Permanent plot markers were placed inside each crater for future identification. These craters were examined again in March 2015 with both the presence and percent cover of the vascular plant species, inside and outside the craters, being recorded.

To examine how the vegetation on Mt. Tongariro is recovering since the 2012 eruptions, 13 of these craters were examined with the presence and percent cover of the vascular species inside and outside the craters recorded. Craters 9 and 11 could not be located or identified and were therefore excluded from the present study. Consistent methodology was used to examination the succession of species affected by ballistic projectiles over the four year period.

A Garmin Oregon 750t handheld GPS device was used to locate the craters from original GPS co-ordinates. Permanent plot markers were then used as a visual confirmation of the correct crater. In cases where permanent plot markers could not be located, such as where the walls of the craters had collapsed and potentially covered the markers; or craters had filled over time, other distinguishing visual features were sought (e.g. a large rock in a particular location: Figure 4.4).

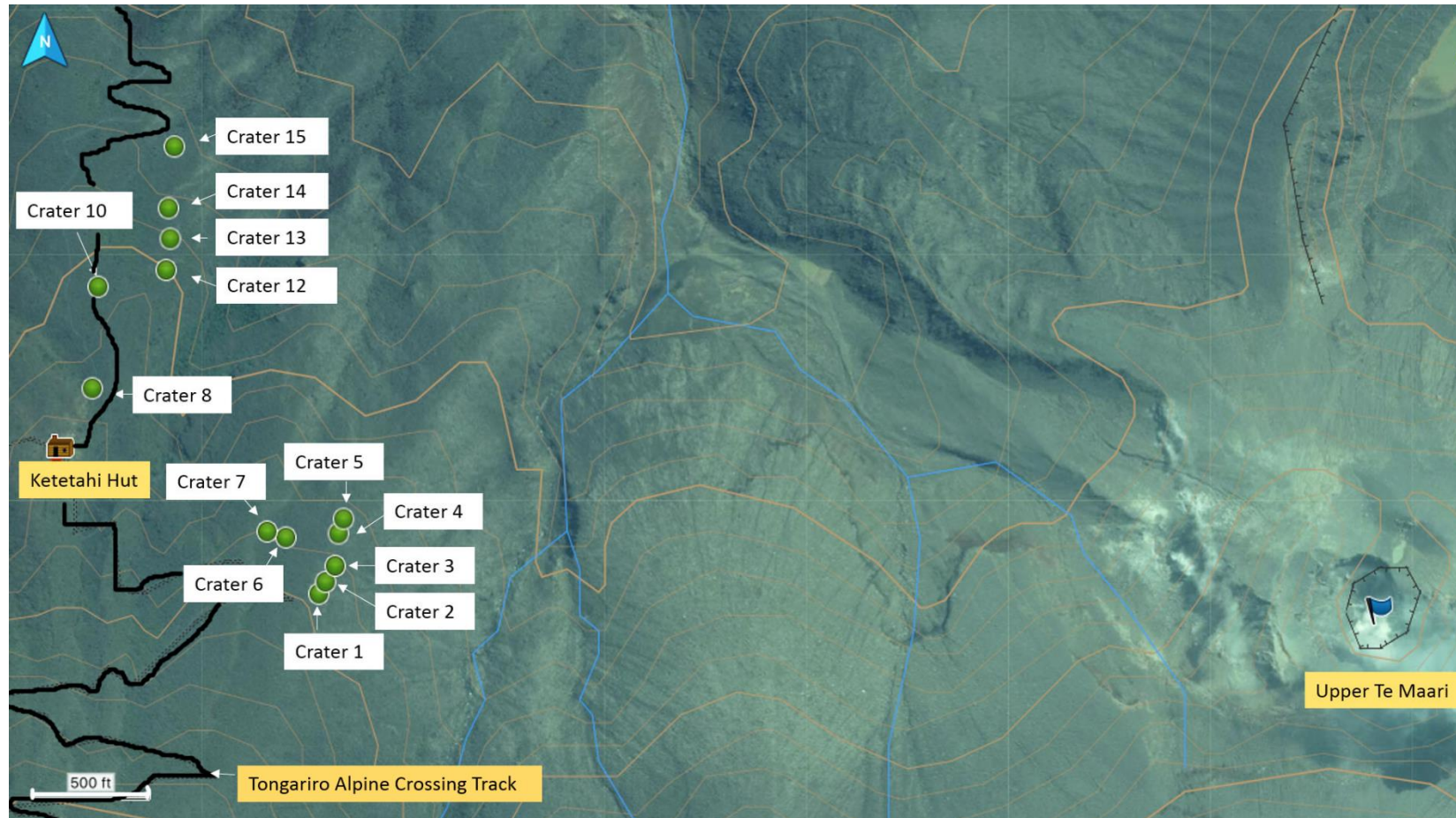


Figure 4.3: Location of craters with respect to Te Maari and the Ketetahi hut.



Figure 4.4 Crater 4 photographed in 2013 (courtesy Jackson Efford), 2015 (courtesy of Rebecca Bylsma) and 2017; showing landscape changes and how landscape features can be used to identify a crater if permanent markers are not visible.

If no clear visual confirmation existed, diameter measurements of the craters in the immediate vicinity were matched with original measurements to locate the study crater. If multiple craters existed with similar diameter measurements, it was concluded that no confirmation was possible and that crater was eliminated from the data set (e.g. Crater 11). The substrate was not disturbed in search of potentially buried permanent markers, in order to minimise the damage and human effect on vegetation inside the craters. Immediately after confirmation of a crater, a peg was placed into the ground 1 m from the rim of the crater, away from the crater centre. This process was repeated multiple times around the outside of the crater, with no more than 1 m between each peg. String was then drawn through the top of these pegs creating a visual string line as a 1 m perimeter around the crater rim. Vascular species which had foliage located inside the crater (including the walls of the crater) were then recorded as being present “inside” the crater, including those rooted outside the crater rim. Species of all layers were recorded, even if visually obscured by another species or other non-living material. The same protocol was then used to record the species present within the 1 m perimeter of the crater rim. These species were recorded as the “outside” crater species data set. Percent cover was estimated for species found inside and outside the crater. Species with less than 1% cover, or those obscured from view, were not assigned a cover rating. All care was taken to minimise damage to the vegetation and substrate.

4.3 Statistical analysis

Data analysis was performed using both Statistica 13.2 (2016) and IBM SPSS Statistics (2017) to ensure results were consistent. Data sets were checked for normality using the Shapiro-Wilks test, and checked for homogeneity with both the Levene’s and Browns-Forsythe tests. The following appropriate statistical analyses were then conducted on the data sets based on these checks (Table 4.1):

Table 4.1 List of statistical analyses performed on data sets including species codes used in the following graphs.

Data set	Test
Mean species richness inside the craters	Kruskal-Wallis
Mean species richness outside the craters	ANOVA
Mean percent cover outside the craters	ANOVA
Mean percent cover for <i>Dracophyllum recurvum</i> (dracrec) outside the craters	Welch's ANOVA
Mean percent over for <i>Celmisia spectabilis</i> (celspe), <i>Chionochloa rubra</i> (chirub), <i>Hebe tetragona</i> (hebtet), <i>Gaultheria colensoi</i> (gaucol), <i>Lepidothamnus laxifolius</i> (leplax), <i>Podocarpus nivalis</i> (podniv) and <i>Coprosma cheesemanii</i> (copche) outside the craters.	Kruskal-Wallis

Turkey's post hoc comparison were conducted on ANOVA analyses that showed significance; and pairwise comparisons were conducted on the Kruskal-Wallis analyses that showed significance. These were used to establish where the significance was located.

4.4 Results

4.4.1 Inside the craters.

A change in mean species richness over time is shown in Figure 3.5 (a), with 2013 averaging 1.46 species per crater, 2015 averaging 0.77 species per crater and 2017 averaging 10.15 species per crater. The Kruskal-Wallis analysis indicates at a $p < 0.05$ level, this change in species richness over time is statistically significant $\chi^2(2 = 26.383, p < 0.001)$, with a mean rank score of 15.50 for 2013, 11.73 for 2015 and 32.77 for 2017. The pairwise comparison of group means showed there was a significant difference in the species richness between 2017 and 2013 ($p < 0.001$); as well between 2017 and 2015 ($p < 0.001$). There was no significant difference between 2013 and 2015 ($p = 0.388$).

There is a similar trend in mean percent cover over time with 2013 averaging 2.3% cover per crater, 2015 averaging 0.77% cover per crater and 2017 averaging 13.54% cover per crater (Figure 4.5b).

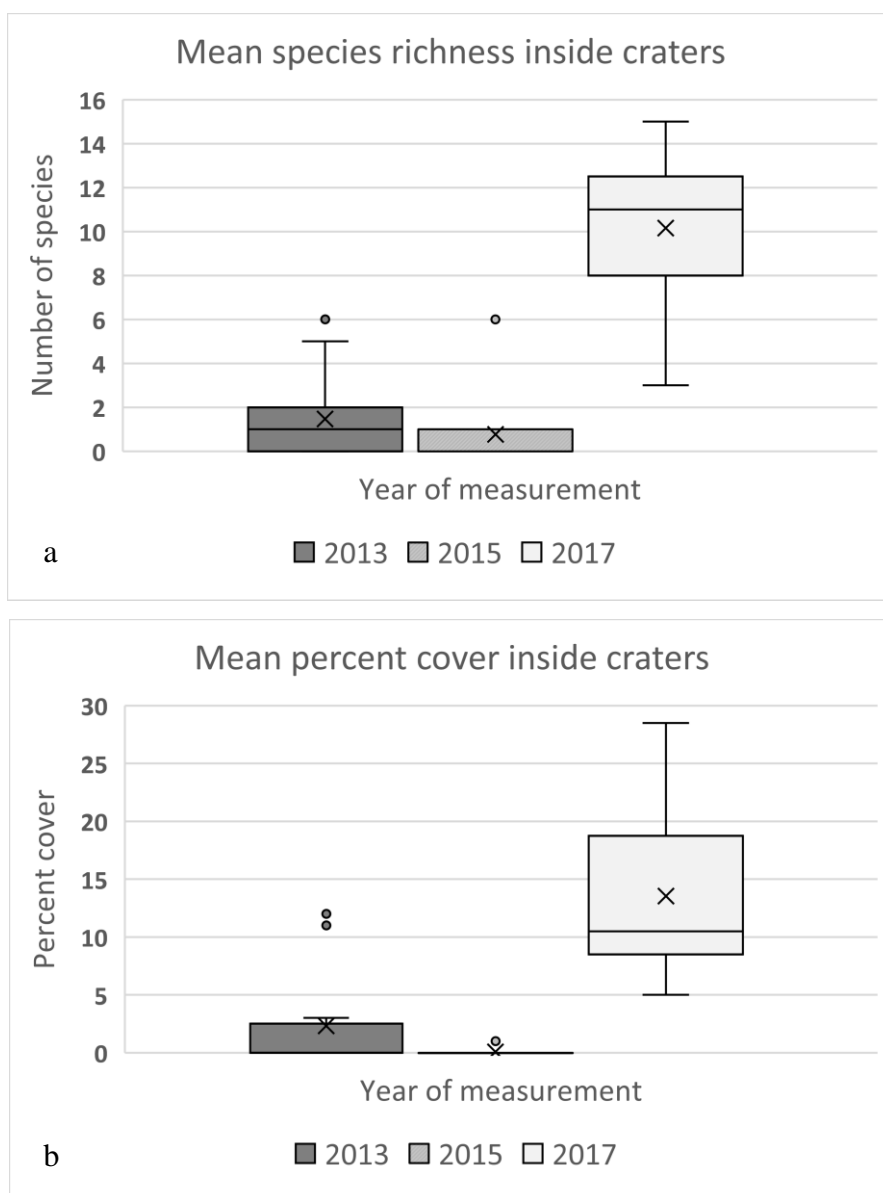


Figure 4.5 The (a) mean species richness and (b) mean percent cover inside the craters for each year of measurement.

Species richness at most craters either remained the same or decreased between 2013 and 2015, with the exception of crater 15 which increased by one species (Figure 4.6a). Between 2015 and 2017 all craters increased in their species richness, with crater 8 increasing by 14 species.

The total percent cover at each crater has a similar trend to the species richness (Figure 4.6b). All craters between 2013 and 2015 either had no change in cover or decreased. Between 2015 and 2017 however, there was a large increase in cover, especially at craters 2, 6 and 8 that showed increases of 28.5, 27.5 and 24.5% respectively.

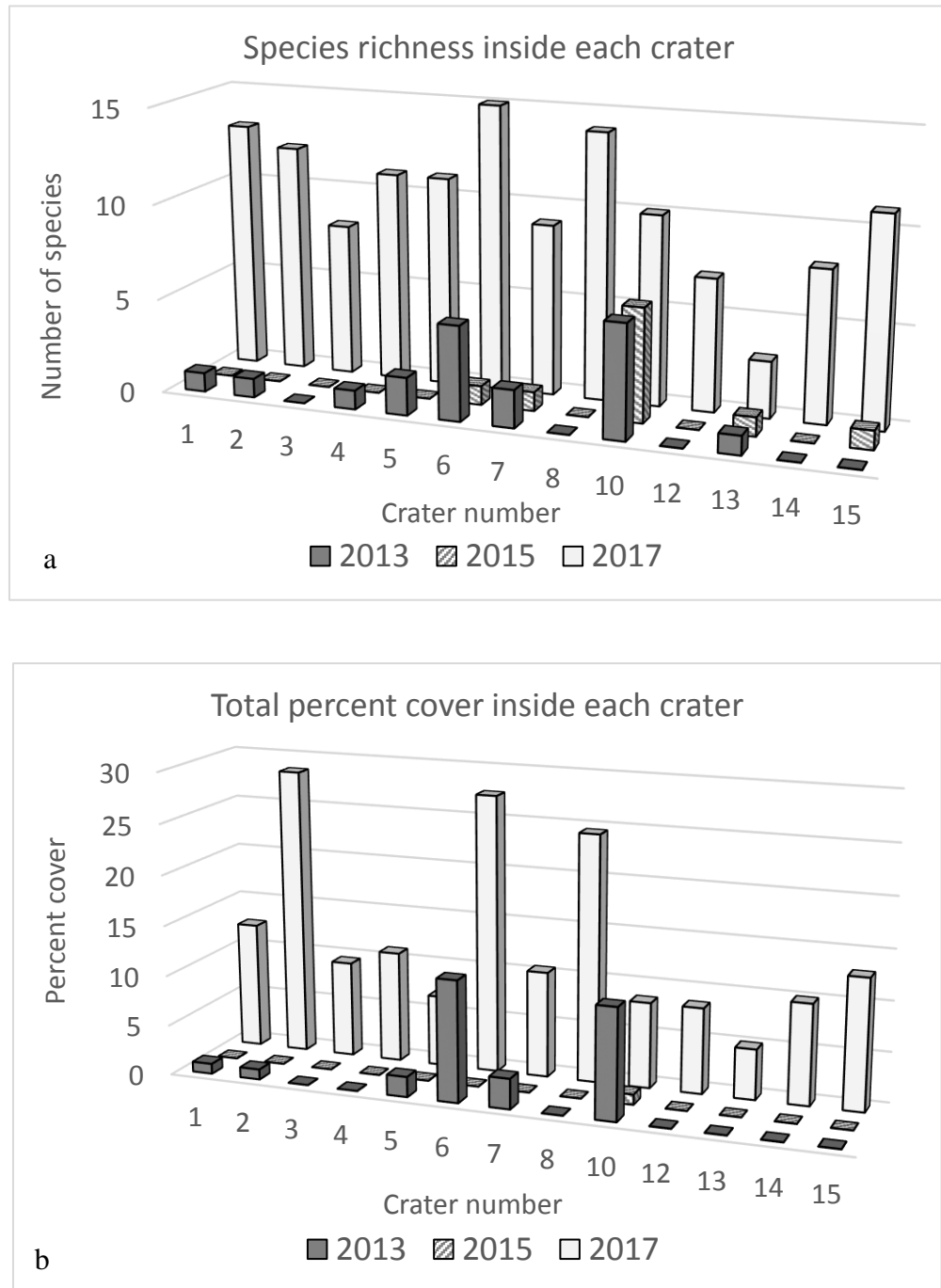


Figure 4.6 Variation at each crater for (a) species richness and (b) percent cover for each year of measurement.

Of the eight most abundant species, seven were present in at least one crater in 2013 but only four were in 2015. All eight species were present in at least half of the craters by 2017, with *Dracophyllum recurvum* located inside every crater (Figure 4.7a). Of these eight species, the mean number of craters they occupied was 3.38 craters for 2013, 0.88 craters for 2015 and 9.38 craters for 2017.

The mean percent cover for these species follows a similar trend to the abundance counts, with seven species showing cover in 2015 but only one species showing cover above zero in 2015 (Figure 4.7b). In 2013 the average cover for these species was only 0.27% with less than 0.01% cover in 2015. In 2017 all species had a mean percent cover above 0.5% with the average being 1.23%, and *Dracophyllum recurvum* the largest mean percent cover of 2.46 %.

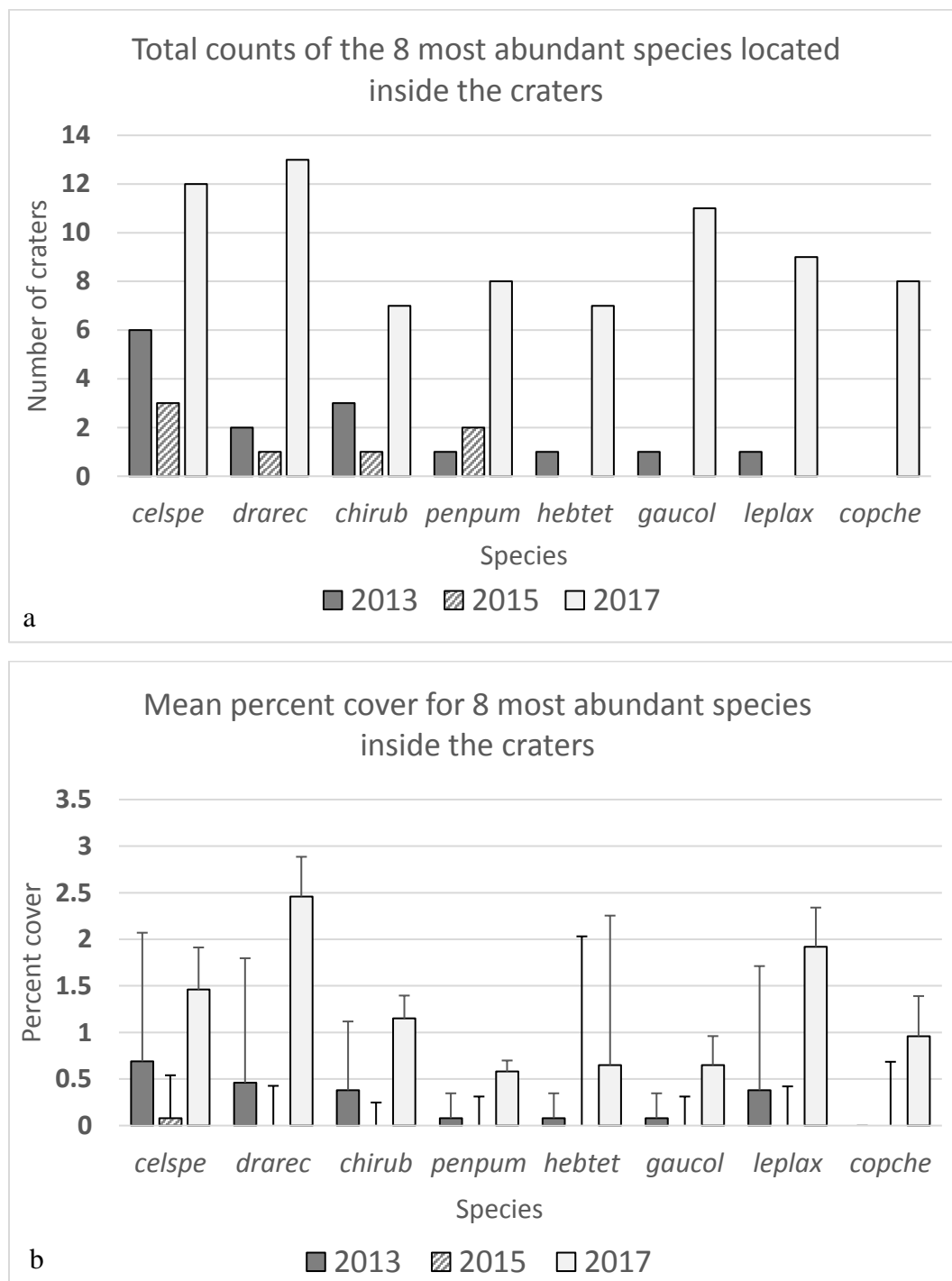
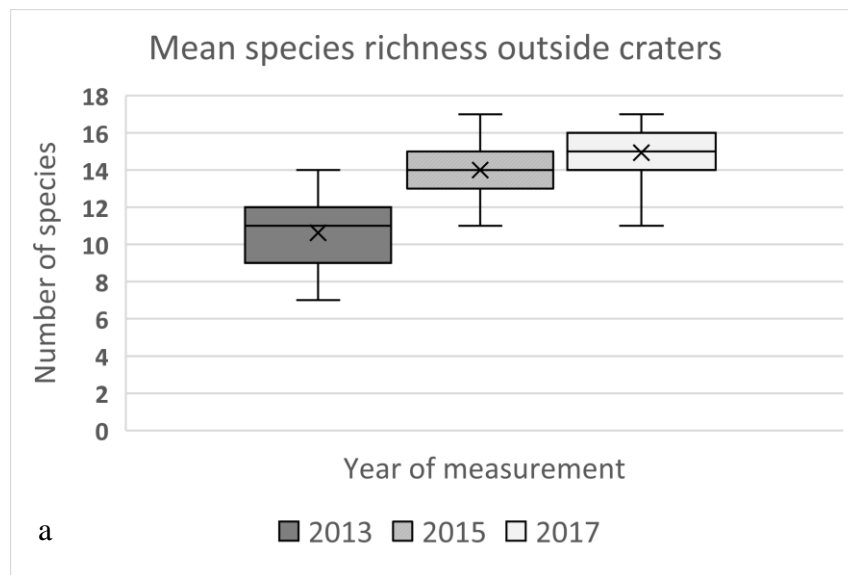


Figure 4.7 The eight most abundant species inside the craters for (a) total number of craters each species is located in (b) mean percent cover of these species.

4.4.2 Outside the craters

The mean species richness increases over time with 2013 averaging 10.61 species per crater, 2015 averaging 14.00 species per crater and 2017 averaging 14.92 species per crater (Figure 4.8a). A one-way ANOVA was conducted and showed this change in mean species richness over time is statistically significant at a $p < 0.5$ level, $F(2,36 = 20.40, p < 0.001)$. A Tukey HSD showed the significance was between 2013 and 2015 ($p < 0.001$) as well as between 2013 and 2017 ($p < 0.001$). The increase between 2015 and 2017 is not significant ($p = 0.404$).

Even though the number of species increased significantly over time, Figure 4.8(b) does not show the same trend in percent cover over time. In 2013 the mean percent cover was 54.46%, in 2015 the mean cover was 51.85% and in 2017 the mean cover was 65.04%. A one-way ANOVA was conducted and showed that at a $p < 0.05$ level, there was no statistically significant difference in mean percent cover over time $F(2,36 = 2.580, p = 0.90)$.



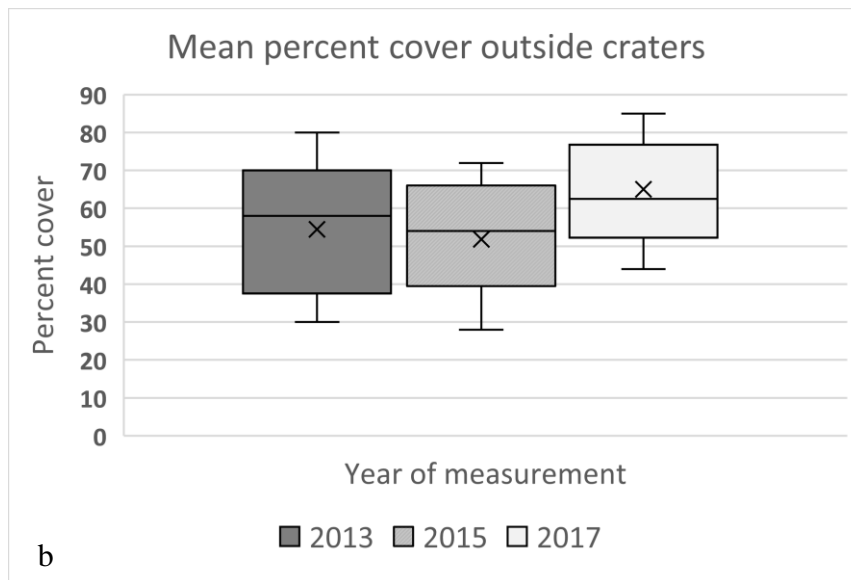


Figure 4.8 The mean species richness (a) and mean percent cover (b) inside the craters for each year of measurement.

The species richness outside all craters increased from 2013 to 2015, however between 2015 and 2017 there is either an increase, decrease or the same richness depending on the crater examined (Figure 4.9a). Craters 4 and 13 show a decrease; Craters 1,2, 3, 7, 8, 10 and 15 show an increase, with the remaining craters showing no change in species richness between 2015 and 2017.

The total percent cover does not follow the same trend (Figure 3.9b) as the species richness. While the species richness at all craters increased between 2013 and 2015, most of the craters showed a decrease in percent cover over the same time. This trend reversed between 2015 and 2017 with all craters except Crater 12 and 14, increasing in percent cover.

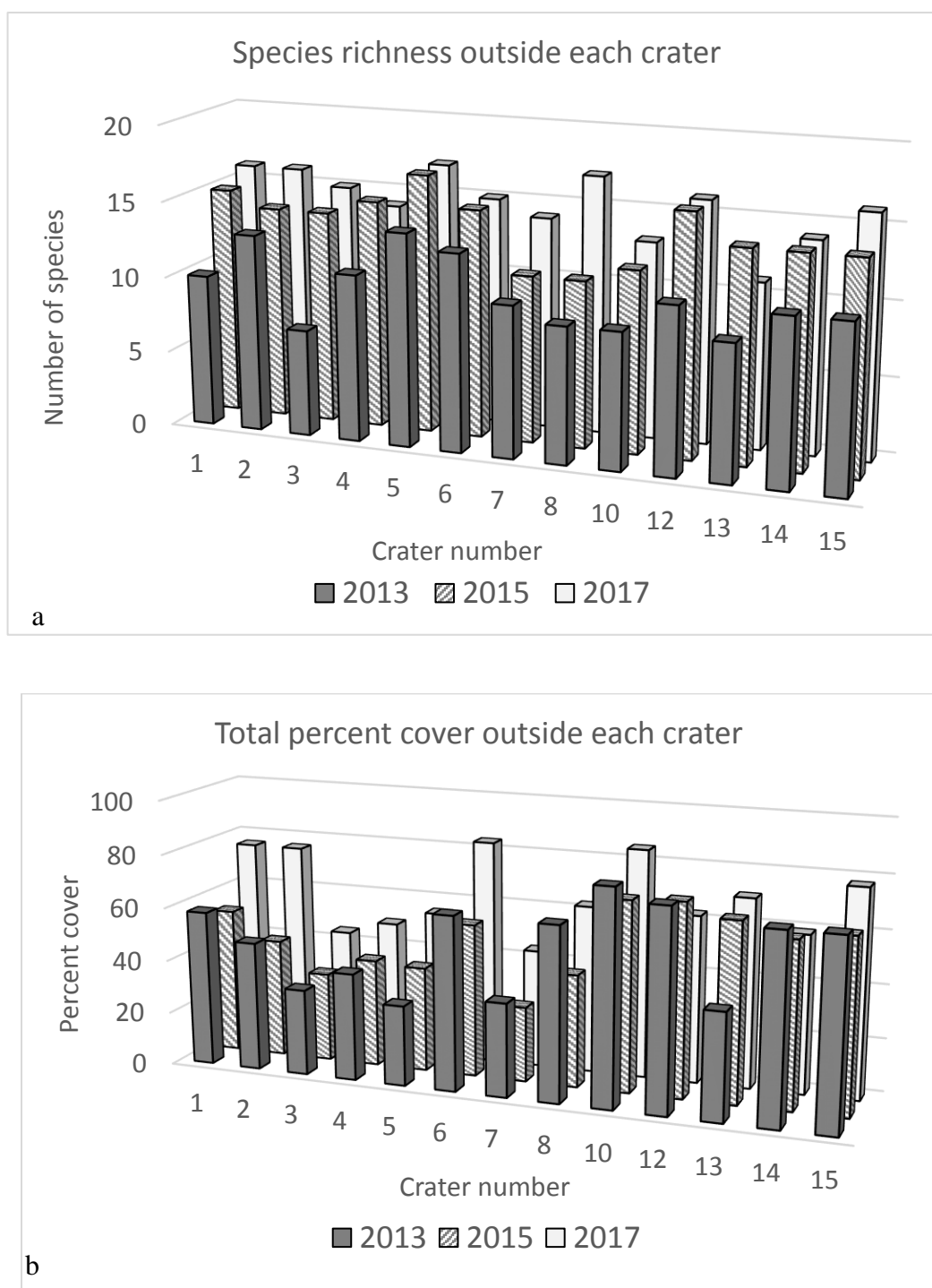


Figure 4.9 Graph (a) shows species richness and (b) the mean percent cover inside the craters for each year of measurement.

The eight most abundant species were present in at least five craters between 2013 and 2015 with *Celmisia spectabilis* present at every crater over the four years (Figure 4.10a). *Chionochloa rubra*, *Hebe tetragona*, *Gaultheria colensoi* and *Lepidothamnus laxifolius* all consistently increased over time, while *Podocarpus nivalis* consistently decreased. *Coprosma cheesemanii* and *Dracophyllum recurvum* both showed increases and decreases overtime. Of these species the mean

number of craters they occupied was 10 craters for 2013, 11.75 craters for 2015 and 12 craters for 2017.

The mean percent cover of each species varied over the four years (Figure 4.10b). In 2013 the mean cover for these species was 6.57%, in 2015 the mean cover was 5.72% and in 2017 the mean cover was 6.54%. *Dracophyllum recurvum* was the species with the highest percent cover in 2013 with 18.45%. The cover had dropped to 9.3% in 2015 and increased slightly to 12.38% in 2017. A one-way ANOVA with Welch's adjusted ratio showed at a $p < 0.05$ level the change over time was statistically significant, Welch's $F(2, 21.794) = 3.717$, $p = 0.041$. Tamhane, Dunnett T3 and Games Howell Post Hoc tests all revealed the only significant results at a $p < 0.05$ level was between 2013 and 2015 ($p = 0.038$, $p = 0.037$, $p = 0.033$ respectively).

Kruskal-Wallis H tests showed a statistically significant change in mean percent cover over time for both *Coprosma cheesemanii* and *Gaultheria colensoi*. Change in *Coprosma cheesemanii* showed significance $\chi^2(2) = 9.156$, $p = 0.10$, with a mean rank score of 12.54 in 2013 and 23.73 in both 2015 and 2017. The pairwise comparisons with Bonferroni correction showed the significant differences existed and were identical between 2013 and both 2015 and 2017 ($p = 0.26$, $p = 0.26$ respectively). Change in *Gaultheria colensoi* showed significance $\chi^2(2) = 23.087$, $p < 0.001$, with a mean rank score of 10.31 in 2013, 18.96 in 2015 and 30.73 in 2017. The pairwise comparison with Bonferroni correction showed the significance was between 2017 and both 2013 and 2015 ($p < 0.001$ and $p = 0.017$ respectively). *Celmisia spectabilis*, *Chionochloa rubra*, *Podocarpus nivalis*, *Hebe tetragona* and *Lepidothamnus laxifolius* all showed no statistically significant change in mean percent cover over time.

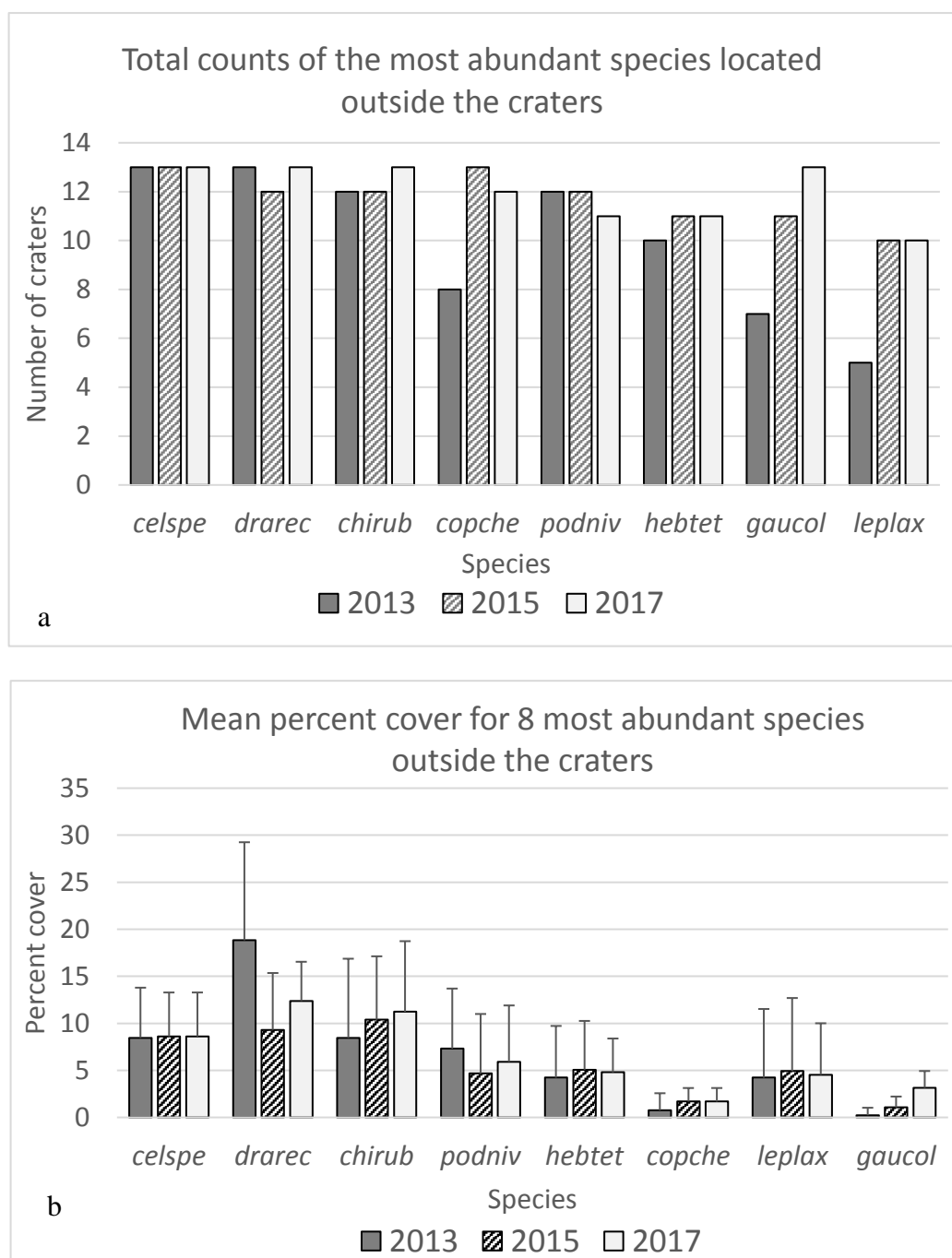


Figure 4.10 The eight most abundant species inside the craters for (a) species richness (b) mean percent cover.

4.5 Discussion

4.5.1 Inside the craters

Since the eruption 4.5 years ago, there has been a significant change for both the mean species richness and the mean percent cover inside the craters. The change includes a decrease for both species richness and percent cover from 2013 to 2015

(Figure 4.5), though these decreases were not statistically significant. An examination of the data at a crater level shows that a decrease in species richness occurred in most craters, with only one crater increasing by one species (Figure 4.6a). The mean percent cover data was more consistent with all craters showing a decrease in cover (Figure 4.6b). This consistency of results, at a crater level, supports the validity of the trends shown. The eight most abundant species (Figure 4.7) also supports these trends as all species except *Pentachondra pumila* decreased in the number of craters they were located in, and all species decreased in their mean percent cover. This consistency of results, at a species level, also supports the validity of the trends shown.

These consistent decreases lead to speculation that the vegetation did not die immediately on impact during the eruptions, but within the first 2.5 years, it experienced a slow and/or delayed dieback. As dieback was delayed, death from the PDCs (heat damage) is unlikely. Species within the tussock-shrublands lower on Mt. Tongariro (see chapter 2) showed species browned immediately and death then followed shortly after. No browning of species was observed inside the craters. These result could therefore be attributed to many factors including:

- 1: The displaced debris could have smothered photosynthetic structures, inhibiting energy production and resulting in death. Mack (1981) found after the Mt. St. Helens eruption that mechanical overloading from ash affected acaulescent or prostrate species survival significantly. The dieback trend found in the present study however is consistent for all growth forms include tussock, therefore mechanical overloading is unlikely to be the sole cause of die back.
- 2: The ash fall in November 2012 could have changed the substrate chemistry beyond the tolerance limit of most species, resulting in the observed dieback. Tephra can change the pH, Na^+ , K^+ , NH_4^+ , SiO_2 , oxygen saturation and redox potential of soil, all of which can effect vegetation survival (Hotes et al. 2004). Ash can also change water availability as the texture is different to soil and can retard water evaporation from the soil surface and increase water retention due to its high porosity (Efford et al. 2014).
- 3: The effect of tephra deposition on vegetation varies with the seasons. Ash fall at the start of a growing season (spring) is more detrimental than when the plants are dormant in autumn (Hotes et al. 2004), as it can interrupt flowering and fruiting (Mack 1981). Seasons also vary in terms of their “abiotic mechanical forces (freeze-

thaw cycles, wetting-drying cycles and erosion)” which can effect species life processes (Mack 1981). The spring timing of this ash fall could therefore have resulted in the observed slow dieback through suppression of active growth.

4: As stated earlier, extreme temperatures associated with projectile impacts can volatilize the macronutrients in the soil, rendering it oligotrophic and difficult to recolonise (Cockell et al. 2003). If the nutrient levels in the craters were reduced to a level below the species nutritional requirements, this may have resulted in the observed dieback. The temperatures involved with the creation of the impact craters investigated in this research are unknown.

This trend changed with a statistically significant increase in mean species richness between 2015 and 2017 (Figure 4.5). The increase of 0.77 species per crater in 2015 to 10.15 species per crater in 2017, was an increase of more than 10 times the number of species in a two year period. The mean percent cover also increased significantly from 0.77% in 2015 to 13.54% in 2017. These increases for both species richness and mean percent cover were found inside every crater (Figure 4.6). Each of the eight most abundant species also showed an increase in both the numbers of craters they were located in, and their mean percent cover at each crater (Figure 4.7). The consistency of the increase at both a crater and species level, supports the validity of the trends shown. These results suggest that between 2015 and 2017 the conditions for plant colonisation and establishment were more conducive than between 2013 and 2015. Craters can protect plants from wind, create shade and collect rain or snowmelt, thus often resulting in a richer biota inside the craters than outside (del Moral 1999; Cockell & Lee 2002).

To determine if these results are consistent with current findings, a comparison to similar sites where the species richness and percent cover have been examined is required. Naturally made craters from volcanic projectiles, which have been examined for these changes in species composition, are rare in the New Zealand landscape. At Moawhango, near the Waiohuru Army Camp, craters have been formed through shelling activity not volcanic ballistics. These craters are also located in the subalpine plateaux of the central North Island, are predominantly tussock lands over 1000 m a.s.l (above sea level), with crater diameters on average 2.5 m (Kingett-Mitchell Ltd 1999). Of these craters, those located at “Site A, in Zone 11” are the most comparable; with *Chionochloa rubra* the dominant species,

altitude 1240 m, and minimal modification of vegetation from agricultural activities or feral animals. At these craters, no obvious disturbance beyond the crater margin was noticed. Six months after the shelling the craters were bare, while 18 months after the shelling the mean vegetation cover was 6% ($n=4$), with 97% of species in the craters hawkweed (*Hieracium*). It was predicted that the revegetation of craters is likely to take up to 20 years at these sites (Kingett-Mitchell Ltd 1999).

Although the crater sizes and vegetation are similar in each study, direct comparisons are difficult as the time between the disturbance and crater measurements were somewhat different. The present study provides measurements 6 months, 2.5 years and 4.5 years after disturbance, while the craters formed through shelling at Site A were measured 6 months and 18 months after the disturbance. Both studies suggest a slow rate of colonisation inside the craters within the first 2.5 years ($<10\%$ mean species cover and $n<5$), however with no further species measurements of the craters formed through shelling, an examination into species dieback in the first few years (which was found in the present study) is not possible. A comparison of the projected time for crater revegetation is also difficult. The craters created via shelling have a predicted 20 years vegetation recovery time, however this assumes a relatively linear rate of recovery, which was not found in the present study. An accurate prediction of vegetation recovery time in the present study is therefore not possible. Two further aspects of the present study were not supported by the craters formed from shelling:

- 1: This study also found species outside the craters were affected by ballistic projectiles, however the craters formed via shelling reported no obvious disturbance beyond the crater margins.

- 2: The high rate of *Hieracium* colonisation (an invasive species that is a threat to alpine ecosystems in New Zealand) is not supported by the present study. This genus was not located within the craters of the present study. The composition of the species inside the craters of the present study are the indigenous species which are dominant in the surrounding landscape such as *Chionochloa rubra*, *Dracophyllum recurvum*, *Celmisia spectabilis*, *Podocarpus nivalis* and *Lepidothamnus laxifolius* (Figures 3.5 and 3.8). The low rate of tussock grasses and high rate of *Hieracium* colonisation in the craters formed by shelling was suggested to be due to tussock grasses being poor colonisers of bare soil, favouring a dense layer of organic material for seedling establishment (Kingett-Mitchell Ltd 1999).

The present study however found *Chionochloa rubra* one of the more common colonising species though the level of organic material inside the craters was not measured in the present study.

Naturally produced craters, at a similar altitude, examined for species richness and percent cover can be found internationally on the North Slope of Mt. St. Helens, U.S.A. During the 1980 eruption of Mt. St. Helens, deep pumice deposits were formed, not by ballistic projectiles, but by entrained ice that melted leaving many small depressions or “potholes” as a feature of the landscape. These potholes are located approximately 1300 m a.s.l, and have been examined frequently since 1993 for multiple variables including species richness and percent cover. The results showed 13 years after the eruption, the potholes had a mean species richness of 8.6 species and a percent cover of 2.5% (del Moral 1999). This is a lower rate of colonisation than the present study, which had a mean species richness of 10.5 species per crater and a mean cover of 13.54% after only 4.5 years. The comparison must be viewed cautiously though as potholes sampled in 1993 were on average 28.9 m² and the craters in this study were on average 8.9 m². Twenty years after the eruption on Mt. St. Helens, potholes of a smaller size (4 m²) were sampled on the North Slope. These potholes still showed a similar species richness (11.8 species) to both the 1993 potholes sampled and to the present craters, however the percent cover had continued to increase to 44.6% (del Moral 2009). This suggests the majority of colonising species arrive within the first 5 year of an eruption, and then occupy the surrounding space within the craters. A direct examination of whether this colonisation rate is a linear process, or if there is slow dieback within the first few years as found in the present study, is not possible; as no records were taken during this time. The research by del Moral (2009) also suggests the time frame for revegetation of the crater is greater than the 20 years projected by Kingett-Mitchell, however this is most likely dependant on the size of the crater.

4.5.2 Outside the craters

The mean species richness and mean percent cover of the debris apron (1 m perimeter from the crater) are higher than inside the craters, however these do not follow the same trends over time (Figure 4.8). Between 2013 and 2015 the mean species richness decreased inside the craters, however outside the crater the mean species richness increased from 10.61 species (2013) to 14 species (2015), a

statistically significant increase. During the same time period, the mean percent cover showed the opposite trend and decreased from 54.46% (2013) to 51.85% (2015). These results could be due too:

- 1: A dramatic change in some craters skewing the mean totals over all the craters for species richness and/or percent cover.
- 2: The species present in 2013 are slowly disappearing and the new species arriving in 2015 are occupying some of this space.

Examining the data at a crater level between 2013 and 2015 shows all craters increased in species richness (Figure 4.9). Crater 3 had the largest increase in species richness, doubling from 7 species in 2013 to 14 species in 2015. If we excluded this crater from the data set the mean for 2013 would only increase by 0.3 species to 10.91 species per crater, and the mean percent cover would remain at 14%. The variation at a crater level is therefore not significantly skewing the total for the mean species richness. The decrease in mean percent cover between 2013 and 2015 is also not skewed in that direction by variation at the crater level. In fact, eleven of the thirteen craters actually increased in cover, with one crater remaining constant and only one crater decreasing in cover by 1%. The decrease in mean percent cover between 2013 and 2015 is predominantly due to the statistically significant decrease in cover of *Dracophyllum recurvum* from 18.85% in 2013 to 9.31% in 2015 (Figure 4.10b). The only other species that showed a decrease in mean cover over this time was *Podocarpus nivalis*, which decreased from 7.31% to 4.69% however, this decrease was not statistically significant. This suggests the dieback of *Dracophyllum recurvum* has allowed new species arriving in 2015 to occupy that space and colonise the craters.

The significant dieback of only *Dracophyllum recurvum* must be questioned. The present study shows the damage to *Dracophyllum recurvum* was not within the first 6 months but rather in the 2 years following the first measurement. This again suggests death from the heat of the PDCs is unlikely. As stated in Chapter 3, *D. recurvum* is prostrate, which makes it difficult for PDCs to penetrate and therefore provides resistance to the PDCs increasing abrasions and damage. Leaves are rough on the upper surface and are in a rosette formation at the tip (New Zealand Plant Conservation Network 2017), this may retain ash or PDC particles which could have caused salt damage and minimised photosynthesis, leading to a slow or

delayed dieback. The ash may have also changed the soil chemistry beyond a tolerable point for *D. recurvum*.

At the present time, no national or international studies compare species directly outside (within 1m of the craters rim) with those species inside the crater. del Moral (1999) did compare the potholes created on Mt. St. Helens with the adjacent barren pumice deposits. The centres of these sample areas however were 380 m apart.

4.5.3 Succession

In terms of succession, the successional mechanism for the species inside were the ballistic projectiles, with the displacement of debris the main mechanism for species directly outside the craters. Inside the craters species richness and percent cover in 2013 was higher than 2015, suggesting not all craters were habitats for primary succession. Crater 10 for example had six species and 11% cover in 2013, which was only 6 months after the eruption. Either multiple species colonised this crater in a short period of time, or the entire crater was not a primary habitat after the projectiles impact, but rather a portion of the crater. As multiple craters had higher species richness and percent cover in 2013 than 2015, the later is more plausible. Therefore inside and outside the craters could both be viewed as secondary succession habitats, with varying extents of disturbance.

Establishing successional pathways and which model/s of succession best fit the present study is difficult, particularly inside the craters. Craters vary in size, depth, aspect and surrounding topography. Crater 8 for example is located at the bottom of a bank, is deep and has a large portion of the crater filled with water resembling a “wetland”. Crater 4 (Figure 4.4) however, is now filled with soil and is relatively shallow and dry. The species associated with these craters therefore experience different environmental conditions and levels of continual disturbance. Crater 8 species must be water and shade tolerant while species in Crater 4 must be able to tolerate continued soil deposition, high winds, less shade and drier soil. The extent to which these allogenic process are driving succession versus the extent to which the species are modifying the habitat (autogenic process) is unknown. Without knowing the driving mechanism/s it is therefore difficult to assess which model/s of succession best fit this data. With the large space available inside the craters however it is hard to visualise that the “resource-ratio hypothesis” (Tilman 1985) is

the best fit. In this model intraspecific competition for resources is assumed to be the main driver throughout the process of succession, however with more than 75% of most craters still bare soil available to be colonised, this seems unlikely. With such a large space still available for colonisation it is also difficult at this point in time to determine if Connell and Slatyer (1977) “Facilitation” or “Inhibition” models will best fit the craters. In the “Facilitation” model colonists prepare the environment for later successional species, while in the “Inhibition” model once colonists are established, they inhibit subsequent invasion by other species. Within the last two years, *Celmisia spectabilis*, *Dracophyllum recurvum*, *Chionochola rubra*, *Pentachorda pumila*, *Hebe tetragona*, *Lepidothamnus laxifolius*, *Gaultheria colensoi* and *Coprosma cheesemanii* have shown to be eight of the fastest colonisers inside the craters both in terms of the number of craters colonised and their percent cover. With a large space available, however this colonisation does not necessarily indicate a stronger competitive ability, only an ability to disperse to the area and establish (majority or species wind dispersed some disperse through frugivory). These species may therefore not persist, or may exist with a lower percent cover, once space and resources become limited and competition for these resources increases. In time, when less space is available, we can determine if these colonists make way for new species, and therefore the “Facilitation” model fits the data, or if these colonists persist on the landscape making the “Inhibition” model the best fit.

Outside the craters there is less space available, (approx. 25% available for each craters to be colonised). At the present time similar species as inside the craters appear to be the most abundant, however without a direct comparison with a non-disturbed area, it is difficult to establish which species are “colonists”, and which are later successional species. It is also difficult to therefore determine if species are inhibiting the growth (Inhibition), or if they are preparing the environment for later successional species (Facilitation).

4.6 Summary and Recommendations

The results showed that the mean species richness and mean percent cover were both higher outside the craters than inside, with similar species present inside and outside the craters. Between 2013 and 2015 there was a decrease in both species

richness and percent cover inside the craters. This trend reversed between 2015 and 2017 with a statistically significant increase in species richness, and an increase in percent cover. This suggests that species survived the initial impact of the projectile, but experienced subsequent dieback, followed by regeneration as conditions improved. Outside the craters, there was an increase in species richness with each year of measurement, however, the percent cover decreased from 2013 to 2015 before increasing again in 2017. This decrease was attributed to a statistically significant decrease in the cover of *Dracophyllum recurvum*.

In order to further examination which model/s of succession are applicable and the best fit, a continuation of data collection and comparative photographs every two years is recommended. An expansion of this study to examine species richness and percent cover further from the craters rim, and outside the debris apron is essential. This would allow an investigation into the extent to which the projectiles affected the species composition in the debris apron, through a direct comparison with species in the crater and of non-affected areas of the landscape. It is also recommended to re-measure the depth and diameter of each crater every two years to establish the volume of soil deposition and changes from crater walls collapsing, and therefore the continued disturbance at each crater. An expansion in the both the abiotic and biotic factors investigated is also recommended to included aspects such as soil chemistry, moisture levels and the microorganism composition of the substrate.

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Appendices

APPENDIX THREE

Table A3.1 Detailed crater information. Diameters and depths recorded in 2013.

Crater	easting	northing	Diameters (m)	Maximum depth (m)
1	1829693	5667698	3.1 x 3.2	0.9
2	1829701	5667712	2.3 x 1.6	0.8
3	1829713	5667732	2.2 x 2.6	0.6
4	1829718	5667772	2.7 x 2.8	0.8
5	1829725	5667790	3.3 x 3.3	1
6	1829656	5667769	3.3 x 3.4	1.2
7	1829634	5667778	4 x 3.8	1
8	1829423	5667961	3.9 x 3.3	0.5
10	1829444	5668087	4.3 x 4	0.75
12	1829525	5668105	2.9 x 3.2	0.7
13	1829531	5668144	3.1 x 2.6	0.8
14	1829530	5668182	4 x 2.8	0.7
15	1829539	5668258	5.1 x 4.8	1.2

Table A3.2 Percent cover of the vascular species inside each crater. “+ “ means present but percent cover <1%. Empty cell = species not located at that crater.

2013													
Crater #													
Species	1	2	3	4	5	6	7	8	10	12	13	14	15
celspe		1		+	1	+	2		5				
chirub	1					2			2				
drarec					1	5							
hebtet						+	1						
gaucol									1				
leplax						5							
penpum									1				
aniaro									1				
poacita									1				
Total	1	1	0	0	2	12	3	0	11	0	0	0	0

2015													
Crater #													
Species	1	2	3	4	5	6	7	8	10	12	13	14	15
celspe						+	+		1				
penpum									+				+
chirub											+		
drarec											+		
aniaro									+				
poacit									+				
Total	0	0	0	0	0	0	0	0	1	0	0	0	0

2017													
------	--	--	--	--	--	--	--	--	--	--	--	--	--

	Crater #													
Species	1	2	3	4	5	6	7	8	10	12	13	14	15	
drarec	3	4	3	2	2	5	2	4	+	2.5	1	1.5	2	
celspe	1	1	1	1	1	3	2	1	3	1.5		1.5	2	
gaucol	1.5	1	1	1	+	+	2		+	+		+	2	
leplax	1		1	2	2	6				3	4	5	1	
copche	+	2				2	1.5	6	+			+	1	
penpum	1	1		+	+				2		+	1	2.5	
aniaro	1				+	+	+	1	1	+			+	
chirub	+	3			+	2.5		8	1.5				+	
hebtet	2	1		1	1	2.5	1			+				
copper	2	1.5	1		+	1.5						+		
podniv		10		3	1	4	2							
paesca	+					+						1	1	
poacit		2	1	1				+						
genbel	+					+	+							
myrnum		1	1.5					+						
wahpig				+		+			+					
epaalp									1	1.5			+	
luzban		1		+				1						
hisinc						+	+	+						
ourmap	+				+									
poacit									+					
deyave								+						
hiered								+						
phyalp													1.5	
ourvul						1								
hyprad								1						
schpau								+						
uncsp.								+						
rytgra								2.5						
Total	9.5	24.5	6.5	9	5	22.5	8.5	20.5	8.5	6	4	8.5	11	

Table A3.3 Percent cover of the vascular species outside each crater. “+ “ means present but percent cover <1%. Empty cell = species not located at that crater.

2013													
Crater #													
Species	1	2	3	4	5	6	7	8	10	12	13	14	15
celspe	5	5	5	10	5	5	5	5	20	10	5	10	20
drarec	10	10	10	10	5	30	10	20	40	30	20	20	30
chirub	15	5	5	5	5	5	5	35	10	5		5	10
podniv	5	20	5	10	5	15	15	+		+	10	10	+
hebtet	20	5	5	5	5	5			+	10	+	+	
genbel	+	1			+	+	+		+	+	+	+	
aniaro	+	+		+		+		+	+	+	+	+	
copche						+	+	5	5	+	+	+	+
penpum	+	+	2	+	+		+		5	+		5	+
gaucol	3		+			+			+		+	+	+
gauant		+		+	+	+	+						
leplax					5		+			20		20	10
copper	+	+		+	+	+							
ourvul		+		+	+	+							
orepec		2			+								
brabid							+				5		
leufra										+			+
hiered		+				5		+					
poacol				+									
olenum					+			+					
viosp.								+					
poacit									+				
phyalp													+
calvul													+
Total	58	48	32	40	30	65	35	65	80	75	40	70	70

2015													
Crater #													
Species	1	2	3	4	5	6	7	8	10	12	13	14	15
celspe	8	5	6	12	8	5	5	2	15	6	10	10	20
copche	1	1	1	+	1	3	1	5	4	1	+	2	2
chirub	15	10	5	5	3	10		20	22	10	20	5	10
drarec		2	8	7	3	10	4	15	22	15	10	10	15
podniv	2	20	1	8	2	15	10	+		+	+	1	2
aniaro	+	+	+	+	+	+	1	+	1	+		+	+
hebtet	20	3	8	4	6	8	3		+	6	7	1	
gaucol	1	1	1	+	1		4		1	+	1	1	3
poacit	3	1	1	1	1			+	1	+	+	4	+
leplax	2		1	+	4	5	+			20	2	25	5
penpum	1	+	+	2	1	1	+			+		+	+
brabid			1	1	4	+	+				5	3	+
copper	1	1	+		1	+				2	+	+	
genbel	+	+		+	1	+	+		+	+			
mueaxi	+	+			1	+		+		+	+		
ourvul	+	+		+	1	+				+			
epaalp									5	12	12	+	7
wahpyg			+		1	+			+				
hiered								+			+		
luzban								+					
calvul									+				+
paesca	+												
phyalp													1
hisinc								+					
raosp.				+									
Total	54	44	33	40	39	57	28	42	71	72	67	62	65

2017														
Crater #														
Species	1	2	3	4	5	6	7	8	10	12	13	14	15	
celspe	7	7	5	13	10	10	3	4	12	8	6	10	20	
chirub	16	18	7	5	4	12	2	28	15	6	20	3	10	
drarec	13	15	10	9	9	19	7	12	22	15	10	10	10	
gaucol	7	3	3	3	3	1	3	1.5	1.5	3	2	3	7	
copche	3	2	1		1	9	4	7	7	+	1.5	2	7	
podniv	4	18	2	4	5	12	18			+	6	4	4	
hebtet	13	5	8	4	6	9	3		1.5	5	6	2		
penpum	1	1	+	3	1	+		1	9	+		1	2	
genbel	+	+	+	+	1	1	+		+	+		+	+	
aniaro	1	1	1.5	1	+	1	+		2	1			1	
leplax	+		2	1	3	7	2			15	10	16	3	
copper	4	2	1	1.5	1	1.5		2		1.5	+	1		
brabid	1		2	2	4	1	1				4	3		
poacit	3	3	2	3	3			2	3				2.5	
epaalp					1				12	8	5	3	6	
myrnum		1					+	1		+			1	
ourvul		+		+	2					+				
wahpyg		+	+						+				+	
deyave	3	+						+						
ourmap	+				1					+				
hiered							1	3						
calvul									+				2	
phyalp													2	
keldie						+								
hyprad						+								
germic							+							
hisinc								+						
schpau								+						
paesca								+						
gonagg								+						
Total	76	76	44.5	49.5	55	83.5	44	61.5	85	62.5	70.5	58	77.5	

Table A3.4 List of all species included in craters data set.

Code	Species name	Family	Common names
aniaro	Anisotome aromatica	Umbelliferae	Aromatic aniseed, Kopoti
brabid	Brachyglottis bidwillii	Compositae	
calvul	Calluna vulgaris	Ericaceae	Heather
celspe	Celmisia spectabilis subsp. spectabilis	Compositae	Mountain daisy
chirub	Chionochloa rubra subsp. rubra var. rubra	Gramineae	Red tussock
copche	Coprosma cheesemanii	Rubiaceae	
copper	Coprosma perpusilla	Rubiaceae	
deyave	Deyeuxia avenoides	Gramineae	Mountain oat grass
drarec	Dracophyllum recurvum	Ericaceae	Mountain inaka
epaalp	Epacris alpina	Ericaceae	
gauant	Gaultheria antipoda	Ericaceae	Snowberry
gaucol	Gaultheria colensoi	Ericaceae	Snowberry
genbel	Gentianella bellidifolia	Gentianaceae	Gentian
germic	Geranium microphyllum	Geraniaceae	
gonagg	Gonocarpus aggregatus	Haloragaceae	
hebtet	Hebe tetragona	Plantaginaceae	Whipcord hebe
hiered	Hierochloa redolens	Gramineae	Holy grass, Karetu
hisinc	Histiopteris incisa	Dennstaedtiaceae	Water fern
hyprad	Hypochaeris radicata	Compositae	Cats ear
keldie	Kelleria dieffenbachii	Thymelaeaceae	
leplax	Lepidothamnus laxifolius	Podocarpaceae	Pigmy pine
leufra	Leucopogon fraseri	Ericaceae	Patotara, dwarf mingimingi
luzban	Luzula banksiana	Juncaceae	
mueaxi	Muehlenbeckia axillaris	Polygonaceae	Creeping pohuehue
myrnum	Myrsine nummularia	Primulaceae	Creeping matipo
olenum	Olearia nummulariifolia	Compositae	
orepec	Oreobolus pectinatus	Cyperaceae	Comb sedge, cushion sedge, flat-leaved comb sedge
ourmap	Ourisia macrophylla	Plantaginaceae	Mountain foxglove
ourvul	Ourisia vulcanica	Plantaginaceae	Mountain foxglove
paesca	Paesia scaberula	Dennstaedtiaceae	Ring fern, Scented fern
penpum	Pentachondra pumila	Ericaceae	
phyalp	Phyllocladus alpinus	Podocarpaceae	Mountain toatoa
poacit	Poa cita	Gramineae	Silver tussock
poacol	Poa colensoi	Gramineae	Blue tussock
podniv	Podocarpus nivalis	Podocarpaceae	Snow totara
raosp.	Raoulia sp.	Asteraceae	
schpau	Schoenus pauciflorus	Cyperaceae	Bog rush, Sedge tussock
uncsp.	Uncinia sp.	Cyperaceae	
vertet	Veronica tetragona	Plantaginaceae	Whipcord hebe
viosp.	Viola sp.	Violaceae	
wahpyg	Wahlenbergia pygmaea	Campanulaceae	Mountain harebell

Chapter 5

Vegetation development on a debris flow formed by the 2012 Te Maari eruptions

5.1 Introduction

This chapter investigates primary succession on a newly formed debris flow created during the 2012 Te Maari eruptions. The focus of this chapter is determining which species are colonising the debris flow, the extent (rate and cover) of colonisation and the contributing factors. Before presenting the research, relevant background information on the research area and comparative sites is provided.

5.1.1 Research Area

On the 6th of August 2012, a series three short of eruptions occurred near the Upper Te Maari crater on Mt. Tongariro (Figure 5.1). This was the first confirmed eruption of Te Maari since the late 1800s (Scott & Potter 2014) and included a large debris flow, ballistic projectiles, pyroclastic density currents (PDCs), and ash fall. This significant event caused damage to over five km² of the surrounding mature alpine vegetation, which included trees, shrubs, and herbaceous plant communities (Efford et al. 2014; Jolly et al. 2014; Procter et al. 2014).

The debris flow occurred in a southwest direction (Figure 5.2), closely following the contours of the southeast tributary of the Upper Mangatipua stream (Jolly et al. 2014; Lube et al. 2014; Procter et al. 2014). It stretched further than 2 km in distance, inundated an area of 151,000 m² and had a volume of approximately 744,000 m³ (Jolly et al. 2014; Procter et al. 2014). The debris consisted of a matrix of mud-sand, coarse breccia and pebbles to large boulders, which varied in composition with proximity to Te Maari (Procter et al. 2014). The surface of the upper debris flow was also indented by ballistic projectiles creating impact craters within the debris flow (Lube et al. 2014).

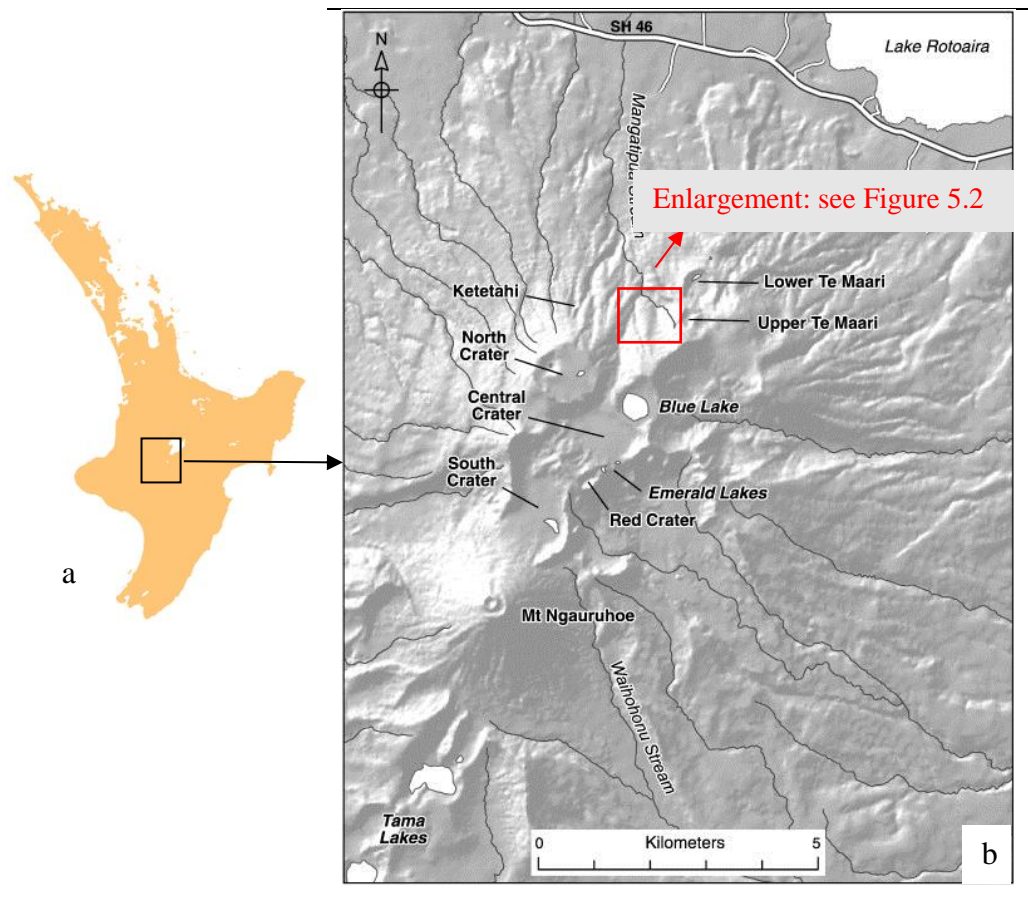


Figure 5.1 (a) North Island of New Zealand, insert indicates the volcanic portion of the Tongariro National Park. Image sourced from <https://en.wikipedia.org/wiki/Pihanga>. (b) Area encompassing Mt. Tongariro, with debris flow area indicated by the red box, and including the Mangatipua stream. Image sourced from Scott and Potter (2014).

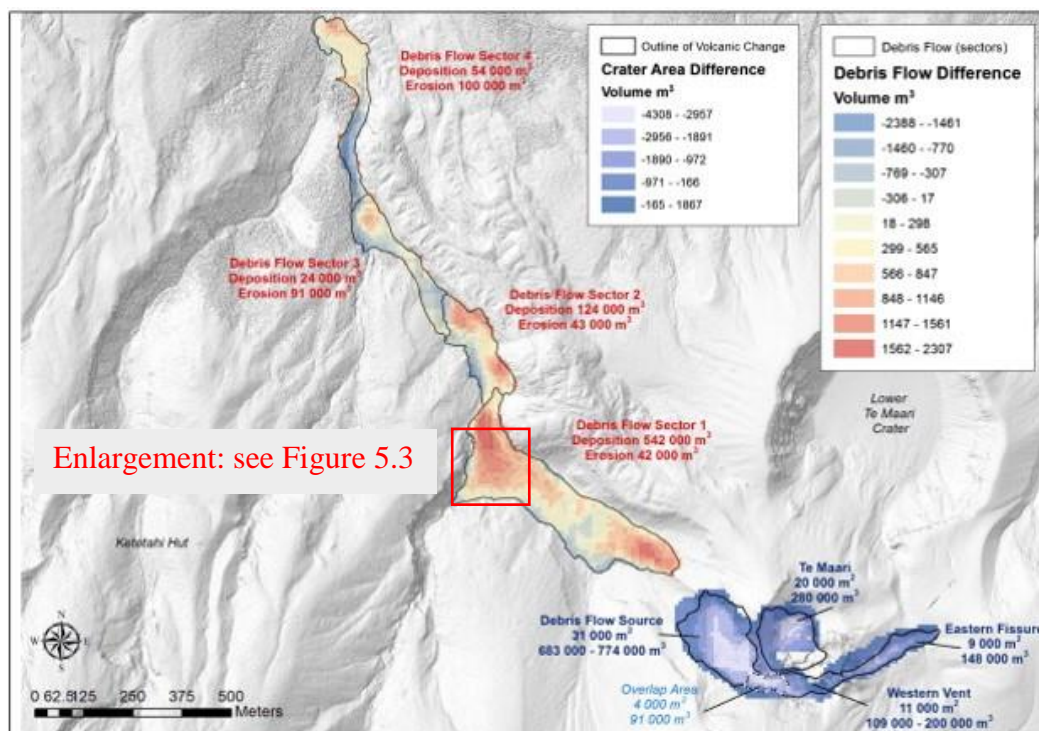


Figure 5.2 Enlargement of the debris flow area, note location of sector 1. Image sourced from Procter et al. (2014).

The volume of deposited debris varied with distance from Te Maari and slope of terrain. The largest deposit occurred in sector 1 of Figure 5.2. (Procter et al. 2014), which created a dam that blocked the flow of three tributaries of the Upper Mangatipua stream. This resulted in the formation of a large lake approximately 140 m in length (Figure 5.3).

On the 13th of October 2012, the dam broke causing a major secondary lahar which damaged part of the Tongariro alpine crossing track and smothered riparian forest further down the mountain (Jolly et al. 2014).

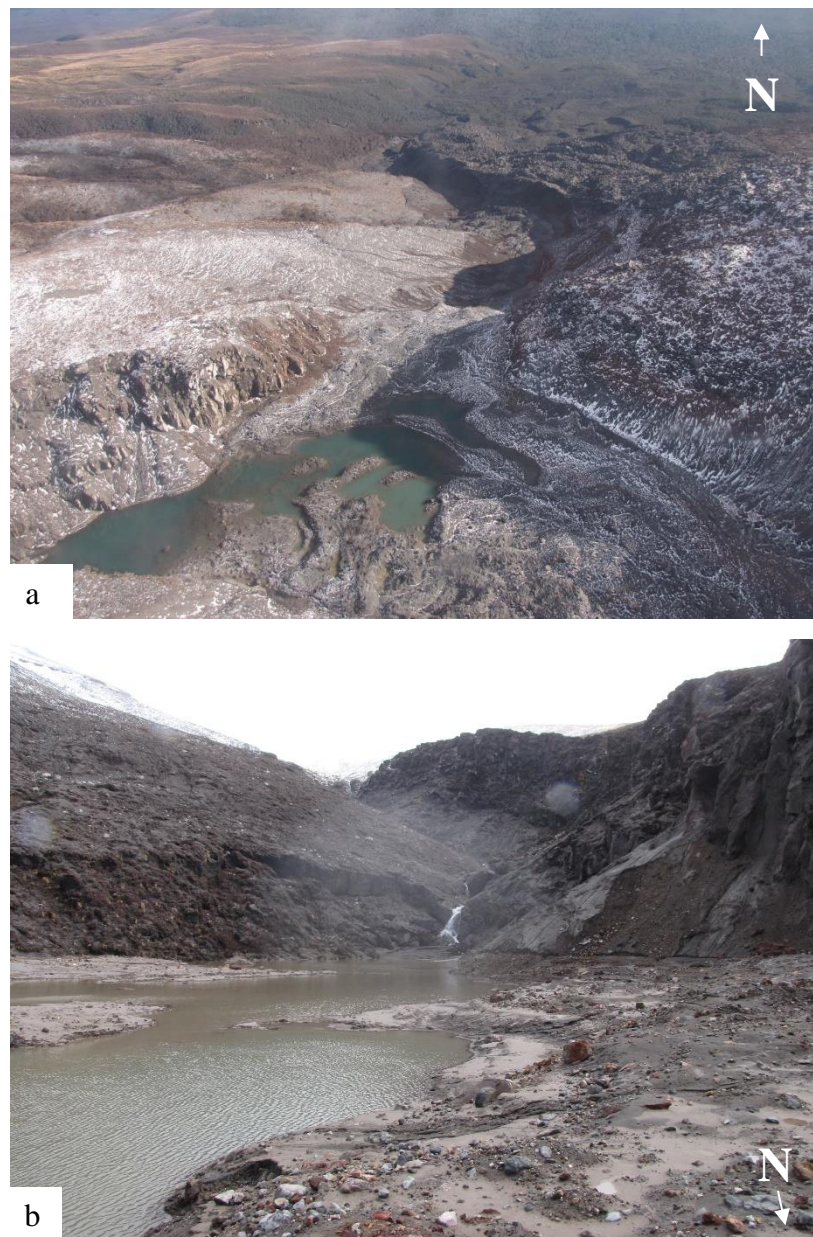


Figure 5.3 The lake formed by the deposition of debris during the eruption. Photograph (a) was taken on the 24th of August 2012, (b) was taken on the 14th of October, the day after the dam broke. Photographs courtesy of Bubs Smith of Ngāti Hikairo ki Tongariro.

The vegetation in the overall eruption zone was examined by Efford et al. (2014), however vegetation recovery on the debris flow was not specifically mentioned. Jolly et al. (2014) also stated “vegetation recovery is occurring but the extent is not yet clear”. This is primarily due to the lack of quantitative research, particularly on the debris flow. Eye witness accounts of the debris flow after the eruptions stated that the magnitude of the debris flow and the resulting change in landscape had produced a surface where primary succession is most probable.

5.1.2 Comparative Sites

A comparison of vegetation development across similar eruption sites is essential in establishing an understanding of driving mechanisms for primary succession. In New Zealand, these are historic sites located within the Tongariro National Park (TNP).

On Mt. Tongariro itself, the only other comparative site is the 1530 A.D. Te Maari lava flow located on the northern slopes. This flow extends from 1400 m to 800 m a.s.l (above sea level). This area was surveyed between 1960 and 1966 by Ian Atkinson with the upper two-thirds of the flow comprised of approximately 30 plant taxa, sparsely distributed and dominated by *Racomitrium lanuginosum* (Atkinson 1981; Clarkson 1990). Between the initial flow event and Atkinson’s survey, this would calculate to a colonisation rate of approximately 0.069 species per year (assuming colonisation is linear).

There are several other sites in the TNP where new surfaces, suitable for primary succession, can occur after eruption events. These are mainly lava flow surfaces rather than debris flows and include the prehistoric lava flow in the Mangatepopo Valley in which 50 plant taxa are present (Clarkson 1990).

Additionally, the adjacent Mt. Ngauruhoe has several lava flows created by eruptions in 1870, 1949, 1952 and pyroclastic flows in 1974-75. The lava flow created in 1870 was stated as being “floristically poor” as it hosted approximately 30 taxa (Clarkson 1990). This would result in a colonisation rate of 0.25 species a year if colonisation is linear. On this flow, grasses, herbs and shrubs were found mainly growing on ash or gravel, with lichens and mosses growing on the larger boulders. In 1966 only two species were recorded on the 1954 lava flow with 4 –

11 taxa being recorded in 1990 on the 1949 and 1954 flows, depending on altitude and substrate size (Clarkson 1990). Even though there had been a significant increase in the number of species and cover by 1990, the “rates of change are still extremely slow” (Clarkson 1990).

Mt. Ngauruhoe’s pyroclastic flow of 1974-75 had a mixture of particle sizes ranging from gravel to boulders, which subsequent debris flows have added too. The number of plant taxa varied from 6 -10 with the various particle sizes, highlighting how the nature of the surface can affect plant colonisation. International comparative studies include Wood and del Moral (1987) and Tsuyuzaki and del Moral (1995), which summarize similar research on areas affected by the 1980 eruption of Mt. St. Helens in Washington state, U.S.A. Within this eruption zone, an area called the Plains of Abraham, and another area near Butte Camp are only 300-350 m higher in altitude than the Te Maari debris flow in the present study. The Plains of Abraham are relatively flat, in a temperate climate, and have experienced pyroclastic density currents, lahars and ice melt. Eight years after the eruption, del Moral and Wood (1993) reported a mean species richness of 0.44 species per plot (100m²) and a cover estimate of 0.04 percent. The mudflow near Butte Camp had newly deposited material and was deep with no survivors. The vegetation at this site was examined by Tsuyuzaki and del Moral (1995) and had 1.5% cover after 6 years, with *Polygonum newberryi* and *Abies lasiocarpa* the leading taxa.

Opportunities to research these ecosystems where primary succession is occurring are rare, and present day knowledge regarding the mechanisms driving this fundamental ecological process is lacking. This has resulted in current models of primary succession being incomplete, difficult to establish and having low predictive power.

The aim of the present study is therefore to increase the understanding of what mechanism/s drive primary succession, particularly following volcanic disturbance, by providing quantitative data that can contribute to development of more accurate models of succession.

Specifically, the objective of this chapter’s research is to examine the vegetation

development on a debris flow formed by the 2012 Te Maari eruption by considering the following research questions:

1. Which plant species have colonised the surface of the debris flow?
2. What is the extent of colonisation?

This includes examination of the presence and percent cover of vascular and non-vascular plant species.

5.2 Methods

Due to safety concerns accessing and sampling all areas within the debris flow, and to eliminate slope as an effect, only relatively flat terrain within sector 1 (Figure 5.2) was examined (Figure 5.4).

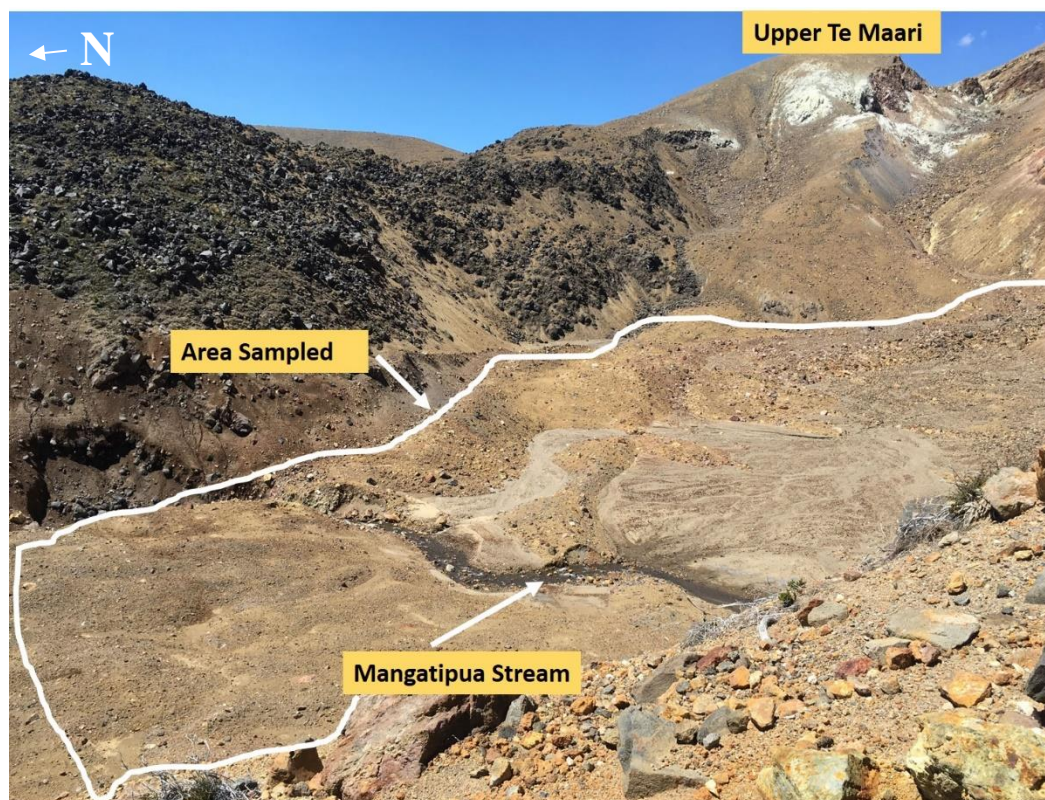


Figure 5.4 Annotated photograph showing the area sampled within the debris flow.

Thirty 2 x 2 m quadrats were evenly dispersed across the sampling area (Figure 5.5), totalling 120 m² of sampled area. This quadrat placement approach was utilised to ensure data was gathered from marginal areas and those in the centre of

the debris flow, as well as areas close to Te Maari and to the location of the lake that formed at the distal end of sector 1.

Identically uniform distances between quadrats were not possible due to varying terrain (e.g. steep slopes or pooled water). Species' presence, including mosses and lichens, were recorded along with visual estimates of percent cover for each species. Visual estimates were consistently recorded by the primary researcher to minimise any subjective bias.

Care was taken to minimise damage to the vegetation and substrate by not moving the substrate (such as silt and rocks) in order to identify the species, or for photographs.

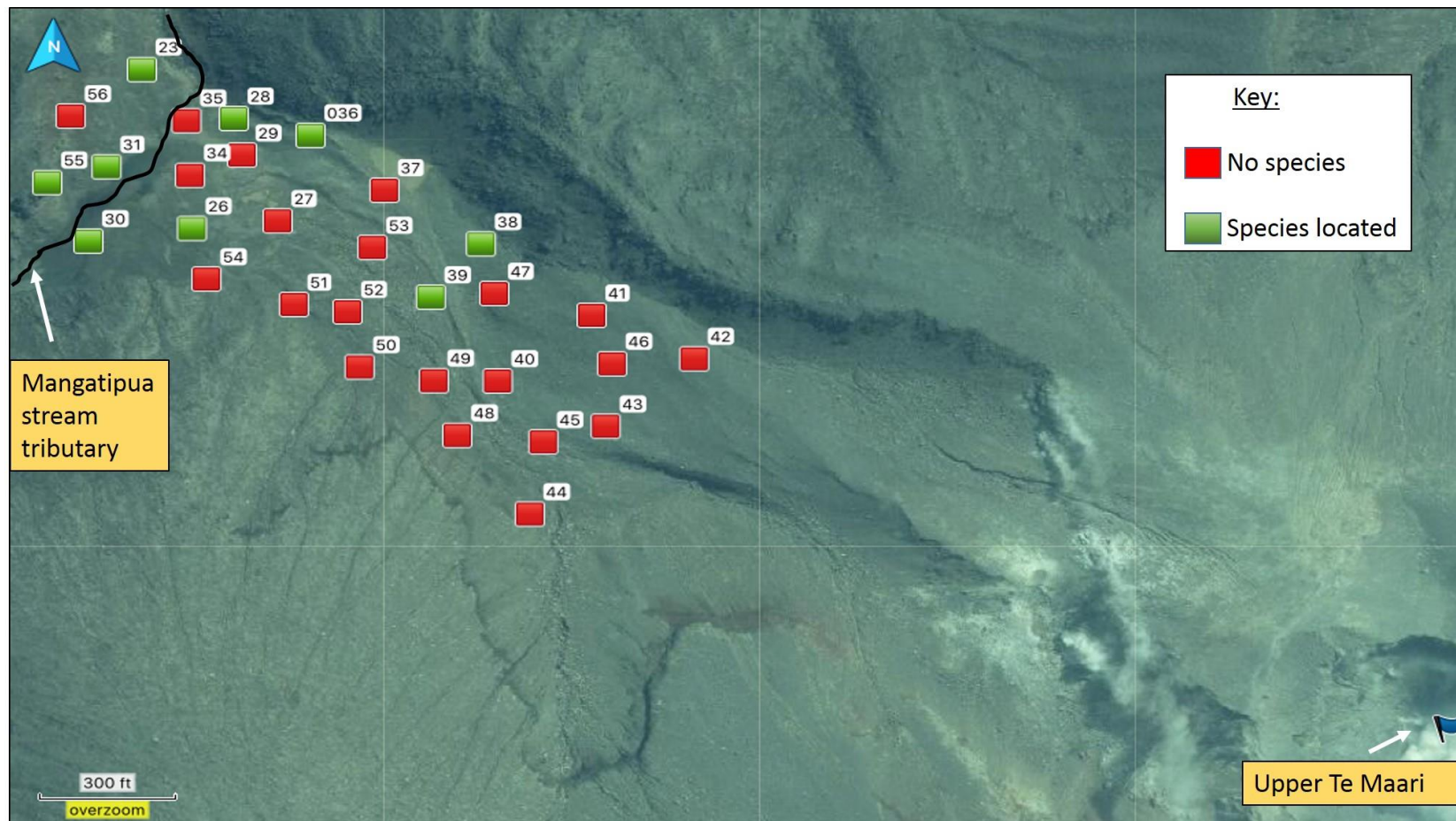


Figure 5.5 Image showing the quadrat locations, their proximity to Te Maari, and the Mangatipua tributary stream.

5.3 Results

Of the 30 quadrat locations sampled, only nine contained any plant species, seven of which contained vascular plants. There were seven records identified to species level, and three identified to genus. One record could only be identified to family level (Table 5.1).

For those quadrats containing species, the richness ranged from one to six species per quadrat. The mean species richness over all 30 quadrats sampled was 0.63 species/quadrat, which is a colonisation rate of 0.14 species per year for the entire debris flow. The mean percent cover for all thirty quadrats it was 0.25%, and the most frequent and abundant genus was *Poa*.

Quadrat identification numbers are listed in Table 5.2 and corresponding locations shown in Figure 5.5.

Table 5.1 Summary of species located on the surface of the debris flow in sector 1. Mean cover (%) is the average percent cover for that species in quadrats it was located in.

Species	No of quadrats	Mean cover (%)	Life form	Main dispersal mechanism
Lichen	1	0.1	lichen	wind
<i>Campylopus</i> sp.	2	0.3	moss	wind
<i>Luzula banksii</i>	2	0.2	sedge	wind
<i>Racomitrium lanuginosum</i>	1	0.5	moss	wind
<i>Poa</i> sp.	4	0.6	grass	wind
<i>Poa cita</i>	1	9.0	grass	wind
<i>Coprosma perpusilla</i>	1	0.1	subshrub	bird
<i>Chionochloa rubra subsp. rubra var. rubra</i>	2	0.6	grass	wind
Grass sp.	2	0.4	grass	wind
<i>Epilobium pernitens</i>	1	0.1	dicot herb	wind
<i>Senecio vulgaris</i>	1	0.1	composite herb	wind

Table 5.2 Location of species on the surface of the debris flow. At the bottom of the table, Average percent cover (quadrats) is the average percent cover for quadrats that contained species. Average percent cover (total) is the average percent cover for all 30 quadrats sampled.

Quadrat ID	Species	% Cover
38	Lichen	0.1
39	<i>Campylopus</i> sp.	0.5
36	<i>Luzula banksii</i>	0.2
	<i>Racomitrium lanuginosum</i>	0.5
	<i>Poa</i> sp.*	0.8
26	<i>Poa cita</i>	9
	<i>Poa</i> sp. *	2
30	<i>Coprosma perpusilla</i>	0.1
	<i>Luzula banksii</i>	0.2
	<i>Chionochloa rubra</i> subsp. <i>rubra</i> var. <i>rubra</i>	1
	Grass sp. *	0.2
	<i>Campylopus</i> sp	0.1
	<i>Epilobium pernitens</i>	0.1
28	<i>Poa</i> sp. *	0.1
31	<i>Senecio vulgaris</i>	0.1
	<i>Poa</i> sp. *	0.3
55	<i>Chionochloa rubra</i> subsp. <i>rubra</i> var. <i>rubra</i>	0.1
	<i>Poa</i> sp. *	0.1
23	Grass sp. *	0.5
Average cover (quadrats)		0.84
Average cover (total)		0.25

* Species identification not possible due to a lack of distinguishing features. These individuals were either juveniles or covered by substrate.

5.4 Discussion

At the time of data collection in April 2017, it was approximately 4.5 years since the Te Maari eruption and resulting debris flow. The results show little colonisation of the area during that time, which is similar to other studies (Table 5.3).

Table 5.3 Comparable national and international eruption studies. For colonisation rate calculations, it was assumed that colonisation rates are linear. Dash indicates data not available.

Study location	Eruption year	Colonisation rate (species per year)	% cover per year	Citation
Te Maari lava flow	1530AD	0.069	-	(Atkinson 1981; Clarkson 1990)
Mangatepopo Valley lava flow	Prehistoric	< 0.1 (based on 50 taxa in 1990)	-	(Clarkson 1990)
Mt. Ngauruhoe lava flow	1870	0.25	-	(Clarkson 1990)
Mt. Ngauruhoe lava block	1954	0.17	-	(Clarkson 1990)
Mt. Ngauruhoe lava flows	1949 and 1954	0.1 – 0.31	-	(Clarkson 1990)
Mt. Ngauruhoe's pyroclastic flow	1975	0.4 – 0.67	-	(Clarkson 1990)
Mt. St. Helens: The Plains of Abraham	1980	0.06	0.005	(del Moral & Wood 1993)
Mt. St. Helens: Near Butte Camp	1980	3.5	0.25	(Tsuyuzaki & del Moral 1995)
Te Maari debris flow	2017	0.14	0.19%	present study

The colonisation rate and percent cover of vegetation in the present study is similar to findings of international studies. Tsuyuzaki and del Moral (1995) stated that pioneer stages of succession on volcanoes are often dominated by perennial herbs, which is consistent with the present study. The dominant genus *Poa* was primarily located in the gravel, with lichens and mosses growing on the larger boulders. This is similar to the locations of grass and non-vascular plants on the neighbouring 1870 Mt. Ngauruhoe lava flow.

The mechanisms driving these plant colonisations should be examined in order to further understand what drives primary succession. del Moral and Wood (1993) suggested that “The path of early succession depends upon the spatial position and dispersal abilities of species in the seed pool, and may not reflect environmental gradients”. However, in the present research, colonisations are predominantly near the Mangatipua stream tributary, implying the environmental gradient of moisture may be a driving force for recruitment and/or coloniser survival. The stream is almost level with the surrounding substrate (Figure 5.6). As the water level

fluctuates with snowmelt and rain, colonising plants may undergo partial or full submersion.



Figure 5.6 Photograph taken from quadrat 30, facing south towards Mangatipua stream tributary. The photograph illustrates how close the water level is to surrounding substrate, as well as vegetation presence on the surrounding banks.

On visual examination of the surrounding terrain, the dominant genus *Poa* was located on very steep slopes, in direct sunlight, in which partial or full submersion in water was not likely to occur. Other species colonising the debris flow area such as *Coprosma perpusilla* were located in drier areas approximately 200 m from the debris flow, implying they required less water for survival. Instead of water availability, mechanisms allowing these species to colonise further afield may have been spatial positioning and ease of seed dispersal, confirming del Moral and Wood (1993). To investigate this idea, seed dispersal and germination dynamics with respect to the Mangatipua stream are discussed below.

5.4.1 Seed Dispersal

To understand the link between recruitment and the stream/moisture, the proximity of the surrounding species and their ability to disperse to the area requires consideration. Walker (1999) states that “colonists are drawn from species that can reach a site” and that “dispersal barriers clearly affect the recovery of primary volcanic surfaces”. At the eastern end of the debris flow (closer to Te Maari and at

a higher elevation), the area is narrow, surrounded by relatively high terrain on three sides and has very little vegetation (Figure 5.7a). Seed dispersal from this area is therefore likely to be minimal. The western end of the debris flow however is wider and more open (Figure 5.7b), with the surrounding terrain containing more vegetation and higher propagule pressure (Figure 5.6). This reasoning is supported by Bullock et al. (2002) who stated there is direct evidence from studies which “have linked intersite differences in successional pathways to the proximity of source populations.”

The western end of the debris flow is also the lowest in altitude and is therefore where water will flow. In this scenario, seeds originally dispersed by wind onto other areas of the debris flow may be transported by rain or snow melt water. Seeds dispersed onto land further upstream (south of Figure 5.6, higher up the mountain where vegetation was less disturbed from the eruption) may also be washed downstream to this point. Additionally, the lake which was created here directly after the eruption may have collected seeds, which remained on the debris substrate after the dam broke and lake level receded. To determine if an increase in seed abundance near the stream is a contributing factor for the colonisation of this area, further studies of the seed deposition on the substrate should be conducted.





Figure 5.7 Photographs of different angles of the debris flow. Photograph (a) was taken from quadrat 35 facing east towards Te Maari. Photograph (b) was taken from quadrat 54 facing north – northwest, towards the Ketetahi carpark.

5.4.2 Germination

Germination is an important part of colonisation therefore the stream/moisture and the terrain must also be considered. The substrate particle size near the stream is much smaller than sites located near Te Maari. This is most likely due to the weathering of larger boulders near Te Maari or further upstream which then travel downhill towards the stream through rain or snowmelt. Changes in water level of the stream through rain and snowmelt will also weather particles within the vicinity stream resulting in small particle sizes. This creates a range of particle sizes within the landscape. Varying substrate particle sizes were also observed on the lava and pyroclastic flows of Mt. Ngauruhoe; where higher colonisation rates occurred in areas with smaller particle sizes (Clarkson 1990). Anisuzzaman et al. (2001) conducted research on the germination of herbaceous perennials in an alpine zone of Mt Fuji and found that “soil particle size had a great impact on seed germination and seedling growth”. They found the highest percentage of seeds germinated in environments with small particles; which is in agreement with the present study’s findings.

5.5 Summary and Recommendations

Colonisation of the Te Maari debris flow is comparable to other sites in the TNP and internationally, both in terms of the rate of colonisation and the type of species. Sites with the highest species richness and percent cover were located near the moisture of the Mangatipua stream. Substrate particle size and proximity to seed sources appear to be controlling mechanisms of seed dispersal and germination, creating variable rates of colonisation across the debris flow.

The current study does not provide adequate information to determine the successional pathway in full or establish a complete successional model. However, it does contribute to the greater literature on this topic and provide a baseline for further research. Continued investigation into the species composition on this site will be helpful, along with data collection on abiotic and biotic factors, such as moisture and nutrient levels, and the microorganism composition of the substrate. This further recommended research would provide a better understanding of the mechanism/s that are driving primary succession and provide evidence for discussion of autogenic and/or allogenic factors determining succession.

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Appendices

APPENDIX FOUR

Table A4.1 Details of site locations and species composition.

Site	easting	northing	Altitude (m)	Species	Cover (%)
23	1830128	5668159	1104	Grass sp.	0.5
26	1830156	5668039	1104	<i>Poa cita</i>	9
				<i>Poa</i> sp.	2
27	1830211	5668043	1105		
28	1830185	5668120	1104	<i>Poa</i> sp.	0.1
29	1830190	5668092	1103		
30	1830091	5668031	1102	<i>Coprosma perpusilla</i>	0.1
				<i>Luzula banksii</i>	0.2
				<i>Chionochloa rubra</i> subsp. <i>rubra</i> var. <i>rubra</i>	1
				Grass sp.	0.2
				<i>Campylopus</i> sp	0.1
				<i>Epilobium pernitens</i>	0.1
31	1830104	5668086	1103	<i>Senecio vulgaris</i>	0.1
31				<i>Poa</i> sp.	0.3
34	1830157	5668079	1061		
35	1830155	5668120	1059		
36	1830234	5668106	1066	<i>Luzula banksii</i>	0.2
				<i>Racomitrium lanuginosum</i>	0.5
				<i>Poa</i> sp.	0.8
37	1830279	5668064	1069		
38	1830339	5668021	1073	Lichen	0.1
39	1830306	5667982	1072	<i>Campylopus</i> sp.	0.5
40	1830346	5667918	1080		
41	1830407	5667966	1100		
42	1830471	5467932	1113		
43	1830414	5667882	1099		
44	1830364	5667818	1095		
45	1830374	5667872	1092		
46	1830419	5667929	1103		
47	1830346	5667984	1077		
48	1830320	5667878	1088		
49	1830306	5667920	1079		
50	1830259	5667931	1076		
51	1830219	5667979	1067		
52	1830253	5667973	1071		
53	1830270	5668021	1069		
54	1830165	5668000	1063		
55	1830066	5668076	1062	<i>Chionochloa rubra</i> subsp. <i>rubra</i> var. <i>rubra</i>	0.1
				<i>Poa</i> sp.	0.1
56	1830082	5668125	1063		

Chapter 6

Synthesis

6.1 Discussion and Recommendations for future research

This research enhances our understanding of vegetation and species responses to volcanic disturbance and is a baseline for future research investigating successional pathways and models of succession after volcanic disturbance. A review of published and unpublished information shows directly comparable data, both nationally and internationally is rare, and highlights the need for continuing and expanded monitoring to determine the factors driving ecological succession after volcanic disturbance. The acquisition of this knowledge is an area of ecological importance (del Moral & Grishin 1999) and will provide valuable information to develop accurate models of succession for landscape effected by volcanic activity. It can also provide the kaitiaki of this world renowned heritage site with quantitative data to inform management decisions.

6.1.1 Response of *Phyllocladus alpinus* to the 2012 Te Maari eruptions

The present research shows the survival of *Phyllocladus alpinus* varies throughout the eruption zone, with the number of “Live” and “Dead” *P. alpinus* correlated with the distance to the eruption source. Temperature changes associated with the pyroclastic density current (PDC) and/or variations in exposure to the PDC most likely contribute to the varying survival, and is supported by Efford et al. (2014). The present research also demonstrates the age of *P. alpinus* does not affect the rate of foliar recovery after disturbance, and that the number of “Damaged” individuals increases with altitude and plot size, with altitude the stronger correlation. This may be due to the path of the PDC, a change in growth form, and/or an increase in light availability with plot size.

New findings such as these are important to ensure up to date knowledge, particularly of native species, is available for management decisions. Götmark et al. (2016) also highlights the importance of examining shrub growth forms, on a world scale, as they are a large part of the world’s ecosystems and have been neglected. It is recommended that this research be expanded to examine the extent

of the symbiotic mycorrhizal associations, the soil chemistry, moisture, light and temperature fluctuations at each plot. Changes in these factors with altitude will provide a clear understating of which allogenic or autogenic process are driving the recovery of “Damaged” *P. alpinus*.

6.1.2 Species sensitivity to the 2012 Te Maari eruptions

The present research finds species sensitivity to the volcanic disturbance, specifically the PDCs, varies within the eruption zone, with *Phyllocladus alpinus* the most affected and therefore most sensitive species. This research also demonstrates a combination of height and morphological features most likely determines species sensitivity to PDCs, which only partially supports the findings of del Moral and Grishin (1999). Taller species were found to have lower foliar survival, which is contrary to Mack (1981) and Clarkson (1997), however PDCs as the primary volcanic disturbance rather than ash fall most likely accounts for the discrepancy in findings. Small coriaceous or glossy leaves; or narrow flexible leaves appear advantageous morphological features while stiff curved, hairy, scaly leaves and a dense growth form is a disadvantage for foliar survival from PDCs. An increase in data collection is highly recommended for the thorough investigation of non dominant species in the landscape such as *Ozothamnus vauvilliersii*, and *Veronica odora* (shrubs). This would allow for a robust examination of the foliar survival between shrubs and other growth forms/heights.

6.1.3 Vegetation development of impact craters formed by the 2012 Te Maari eruptions

Comparable data of species recovery from ballistic projectiles is limited, especially within the debris aprons, where no relevant published literature is available. As this is a novel area of study, it is inherently important to continue this line of research. These findings have demonstrated the mean species richness and percent cover is higher in the debris apron than inside the craters; however, types of species were similar in both locations. This research also demonstrated species within the craters might have survived the initial impact, and then experienced dieback before recovering. Although “impact events can be regarded as biologically ‘resetting’ events because they render the immediate area of the impact sterile” (Cockell & Lee 2002) this research suggests this may not have occurred and therefore may have

resulted in habitats for secondary succession rather than the expected primary succession. Continued species cover and species richness measurements, supported by photographs, every two years, are recommended for inside and outside the impact craters. It is also recommended that a small sample of soil be collected from each crater during species measurements. The soil should be analysed to determine the nutrient levels and microorganism composition at each crater. Due to variation within the craters position and shape within the landscape, the soil moisture should also be measured. These measurements will better inform if allogenic or autogenic processes are the factors driving changes in species composition. Crater diameter and depth measurements every two years, would inform us of the continual disturbance species are exposed to due to substrate deposition and collapses of the crater walls. The final recommendation for this section of the research is to conduct species cover and species richness measurements outside of the debris apron in an “unaffected” area. This would enable us to directly compare and contrast species composition inside the crater, debris apron and the surrounding landscape and determine the successional pathways associated with volcanic disturbance.

6.1.4 Vegetation development on a debris flow formed by the 2012 Te Maari eruptions

The final chapter of this research presents findings on the species colonising a newly formed debris flow. Opportunities to examine these surfaces where primary succession can occur are rare, particularly in alpine environments. This research therefore contributes valuable, though limited, information towards understanding the successional pathways of primary succession on such surfaces. The findings presented support Tsuyuzaki and del Moral (1995) in that the pioneer stages of succession on volcanoes are often dominated by perennial herbs. The colonisation in the present study may be driven by seed dispersal and topography which is supported by Wood and del Moral (1987). The particle size of the substrate may also effect colonisation by limiting germination, this is supported by Anisuzzaman et al. (2001). Continued data collection on the debris flow is recommended, once every five years, as species colonisation is slow. The same method and sites are recommended to determine the species composition throughout the debris flow. A small collection of soil from each site is also recommended in establishing the nutrient levels, particle size and moisture levels of the soil, as well as determine the microorganism composition. The installation of seed traps at various locations

throughout the debris flow, to establish the number of seeds deposited within the various sections, would also add value to future research. These measurements will again help establish if allogenic or autogenic processes are driving ecological succession and therefore provide a better understanding of the successional pathways and model/s are best associated with primary succession.

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